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WILDLIFE IN AMERICAN CULTURE

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The culture of primitive peoples is often based on wildlife. Thus, the plains Indian not only ate buffalo, but buffalo largely determined his architecture, dress, language, arts, and religion.

In civilized peoples the economic base shifts to tame animals and plants, but the culture nevertheless retains part of its wild roots. This paper deals with the value of this wild rootage.

No one can weigh or measure culture, hence I will waste no time trying to do so. Suffice it to say that by common consent of thinking people, there are cultural values in the sports, customs, and experiences which renew contacts with wild things. I venture the opinion that these values are of three kinds.

First, there is value in any experience which reminds us of our distinctive national origins and evolution, i.e., which stimulates awareness of American history. Such awareness is "nationalism" in its best sense. For lack of any other short name, I will call this the "split-rail value." For example: a boy scout has tanned a coonskin cap, and goes Daniel-Booneing in the willow thicket below the tracks. He is re-enacting American history. He is, to that extent, culturally prepared to face the dark and bloody realities of 1943. Again: a farmer boy arrives in the schoolroom reeking of muskrat; he has tended his traps before breakfast. He is re-enacting the romance of the fur trade. Ontogeny repeats phylogeny in society as well as in the individual.

Second, there is value in any experience which reminds us of our dependency on the soil-plant-animal-man food chain. Civilization has so cluttered this elemental man-earth relation with gadgets and middle-men that awareness of it is growing dim. We fancy that industry supports us, forgetting what supports industry. Time was when education moved toward soil, not away from it. The nursery jingle about bringing home a rabbit skin to wrap the baby bunting in is one of many reminders in folklore that man once hunted to feed and clothe his family.

Third, the conquest of nature by machines has led to much unnecessary destruction of resources. Our tools improve faster than we do. It is unlikely that economic motives alone will ever teach us to use our new tools gently. The only remedy is to extend our system of ethics from the man-man relation to the man-earth relation (1). We shall achieve conservation when and only when the destructive use of land becomes unethical—punishable by social ostracism. Any experience that stimulates this extension of ethics is culturally valuable. Any that has the opposite effect is culturally damaging. For example, we have many bad hunt-

ers with good guns. Such a hunter shoots a woodduck, and then tramples the bejeweled carcass into the mud, lest he fall foul of the law. Such an experience is not only devoid of cultural value, it is actually damaging to all concerned. It does physical damage to woodduck, and moral damage to the hunter, and to all fellow-hunters who condone him. No sane person could find anything but minus value in such "sport."

It seems, then, that split-rail and man-earth experiences have zero or plus values, but that ethical experiences may have minus values as well.

This, then, defines roughly three kinds of cultural nutriment available to our outdoor roots. It does not follow that culture is fed. The extraction of value is never automatic; only a healthy culture can feed and grow. Is culture fed by our present forms of outdoor recreation?

The pioneer period gave birth to two ideas which are the very essence of split-rail value in outdoor sports. One is the "go-light" idea, the other the "one-bullet-one-buck" idea. The pioneer went light of necessity. He shot with economy and precision because he lacked the transport, the cash, and the weapons requisite for machine-gun tactics. Let it be clear, then, that in their inception, both of these ideas were forced on us; we made a virtue of necessity.

In their later evolution, however, they became a code of sportsmanship, a self-imposed limitation on sport. On them is based a distinctively American tradition of self-reliance, hardihood, woodcraft, and marksmanship. These are intangibles, but they are not abstractions. Theodore Roosevelt was a great sportsman, not because he hung up many trophies, but because he expressed (2) this intangible American tradition in words any schoolboy could understand. A more subtle and accurate expression is found in the early writings of Stewart Edward White (3). It is not far amiss to say that such men created cultural value by being aware of it, and by creating a pattern for its growth.

Then came the gadgeteer, otherwise known as the sporting-goods dealer. He has draped the American outdoorsman with an infinity of contraptions, all offered as aids to self-reliance, hardihood, woodcraft, or marksmanship, but too often functioning as substitutes for them. Gadgets fill the pockets, they dangle from neck and belt. The overflow fills the auto-trunk, and also the trailer. Each item of outdoor equipment grows lighter and often better, but the aggregate poundage becomes tonnage. The traffic in gadgets adds up to astronomical sums, which are soberly published as representing "the economic value of wildlife." But what of cultural values?

As an end-case consider the duck hunter, sitting in a steel boat behind composition decoys. A put-put has brought him to the blind without exertion. Canned heat stands by to warm him in case of a chilling wind. He talks to the passing flocks on a factory caller, in what he hopes are seductive tones; home lessons from a phonograph record have taught him how. The decoys work, despite the caller; a flock circles in. It must be shot at before it circles twice, for the marsh bristles with other sportsmen, similarly accoutred, who might shoot first. He opens up at 70 yards, for

his polychoke is set for infinity, and the ads have told him that Super-Z shells, and plenty of them, have a long reach. The flock flares. A couple of cripples scale off to die elsewhere. Is this sportsman absorbing cultural value? Or is he just feeding minks? The next blind opens up at 75 yards; how else is a fellow to get some shooting? This is duck-shooting, model 1943. It is typical of all public grounds, and of many clubs. Where is the go-light idea, the one-bullet tradition?

The answer is not a simple one. Roosevelt did not disdain the modern rifle; White used freely the aluminum pot, the silk tent, dehydrated foods. Somehow they used mechanical aids, in moderation, without being used by them.

I do not pretend to know what is moderation, or where the line is between legitimate and illegitimate gadgets. It seems clear, though, that the origin of gadgets has much to do with their cultural effects. Homemade aids to sport or outdoor life often enhance, rather than destroy, the man-earth drama; he who kills a trout with his own fly has scored two coups, not one. I use many factory-made gadgets myself. Yet there must be some limit beyond which money-bought aids to sport destroy the cultural value of sport.

Not all sports have degenerated to the same extent as duck hunting. Defenders of the American tradition still exist. Perhaps the bow-and-arrow movement and the revival of falconry mark the beginnings of a reaction. The net trend, however, is clearly toward more and more mechanization, with a corresponding shrinkage in cultural values, especially split-rail values and ethical restraints.

I have the impression that the American sportsman is puzzled; he doesn't understand what is happening to him. Bigger and better gadgets are good for industry, so why not for outdoor recreation? It has not dawned on him that outdoor recreations are essentially primitive, atavistic; that their value is a contrast-value; that excessive mechanization destroys contrasts by moving the factory to the woods or to the marsh.

The sportsman has no leaders to tell him what is wrong. The sporting press no longer represents sport, it has turned billboard for the gadgeteer. Wildlife administrators are too busy producing something to shoot at to worry much about the cultural value of the shooting. Because everybody from Xenophon to Teddy Roosevelt said sport has value, it is assumed that this value must be indestructible.

Among non-gunpowder sports, the impact of mechanization has had diverse effects. The modern field glass, camera, and aluminum bird-band have certainly *not* deteriorated the cultural value of ornithology. Fishing, but for motorized transport, seems less severely mechanized than hunting. On the other hand, motorized transport has nearly destroyed the sport of wilderness travel by leaving only fly-specks of wilderness to travel in.

Fox-hunting with hounds, backwoods style, presents a dramatic instance of partial and perhaps harmless mechanized invasion. This is one of the purest of sports; it has real split-rail flavor; it has man-earth drama of the first water. The fox is deliberately left unshot, hence ethical restraint is also present. But we now follow the chase in Fords!

The voice of Bugle-Anne mingles with the honk of the flivver! However, no one is likely to invent a mechanical fox-hound, nor to screw a polychoke on the hound's nose. No one is likely to teach dog-training by phonograph, or by other painless shortcuts. I think the gadgeteer has reached the end of his tether in dogdom.

It is not quite accurate to ascribe all the ills of sport to the inventor of physical aids-to-sport. The advertiser invents ideas, and ideas are seldom as honest as physical objects, even though they may be equally useless. One such deserves special mention: the "where-to-go" department. Knowledge of the whereabouts of good hunting or fishing is a very personal form of property. Perhaps it is like rod, dog, or gun: a thing to be loaned or given as a personal courtesy, or even to be sold man-to-man, as in the guide-sportsman relation. But to hawk it in the marketplace of the sports column as an aid-to-circulation seems to me another matter. To hand it to all and sundry as free public "service" seems to me distinctly another matter. Both tend to depersonalize one of the essentially personal elements in hunting skill. I do not know where the line lies between legitimate and illegitimate practice; I am convinced, though, that "where-to-go" service has broken all bounds of reason.

If the hunting or fishing is good, the where-to-go service suffices to attract the desired excess of sportsmen. But if it is no good, the advertiser must resort to more forcible means. One such is the fishing lottery, in which a few hatchery fish are tagged, and a prize is offered for the fisherman catching the winning number. This curious hybrid between the techniques of science and of the pool hall insures the overfishing of many an already exhausted lake, and brings a glow of civic pride to many a village Chamber of Commerce.

It is idle for the profession of wildlife management to consider itself aloof from these affairs. The production engineer and the salesman belong to the same company; both are tarred with the same stick.

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Wildlife management is trying to convert hunting from exploitation to cropping. If the conversion takes place, how will it affect cultural values? It must be admitted that split-rail flavor and free-for-all exploitation are historically associated. Daniel Boone had scant patience with agricultural cropping, let alone wildlife cropping. Perhaps the stubborn reluctance of the one-gallus sportsman to be converted to the cropping idea is an expression of his split-rail inheritance. Probably cropping is resisted because it is incompatible with one component of the split-rail tradition, free hunting.

Mechanization offers no cultural substitute for the split-rail values it destroys; at least none visible to me. Cropping or management does offer a substitute, which to me has at least equal value, wild husbandry (4). The experience of managing land for wildlife crops has the same value as any other form of farming; it is a reminder of the man-earth relation. Moreover ethical restraints are involved; thus managing game without resorting to predator-control calls for ethical restraint of a high order. It may be concluded, then, that game cropping

shrinks one value (split-rail) but enhances both others.

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If we regard outdoor sports as a field of conflict between an immensely vigorous process of mechanization and a wholly static tradition, then the outlook for cultural values is indeed dark. But why can not our concept of sport grow with the same vigor as our list of gadgets? Perhaps the salvation of cultural value lies in seizing the offensive. I, for one, believe that the time is ripe. Sportsmen can determine for themselves the shape of things to come.

The last decade, for example, has disclosed a totally new form of sport which does not destroy wildlife, which uses gadgets without being used by them, which outflanks the problem of posted land, and which greatly increases the human carrying capacity of a unit area. This sport knows no bag limit, no closed season. It needs teachers, but not wardens. It calls for a new woodcraft of the highest cultural value. The sport I refer to is wildlife research.

Wildlife research started as a professional priestcraft. The more difficult or laborious problems must remain in professional hands, but there are plenty of problems suitable for all grades of amateurs. In the mechanical field, research has long since spread to amateurs. In the biological field the sport-value of amateur work is just beginning to be realized. When amateurs like Margaret Nice outstrip their professional colleagues, a very important new element is added: the element of high stakes open to all comers, the possibility of really outstanding amateur performance.

Ornithology, mammalogy, and botany, as now known to most amateurs, are but kindergarten games compared with researches in these fields. The real game is decoding the messages written on the face of the land. By learning how some small part of the biota ticks, we can guess how the whole mechanism ticks.

Few people can become enthusiastic about research as a sport because the whole structure of biological education is aimed to perpetuate the professional research monopoly. To the amateur is allotted only make-believe voyages of discovery, the chance to verify what professional authority already knows. This is false; the case of Margaret Nice proves what a really enterprising amateur can do. What the youth needs to be told is that a ship is a-building in his own mental dry-dock, a ship with freedom of the seas. If you are a pessimist, you can say this ship is "on order"; if an optimist, you can see the keel.

In my opinion, the promotion of wildlife research sports is the most important job confronting our profession.

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Wildlife has still another value, now visible only to a few ecologists, but of potential importance to the whole human enterprise.

We now know that animal populations have behavior patterns of which the individual animal is unaware, but which he nevertheless helps to execute. Thus the rabbit is unaware of cycles, but he is the vehicle for cycles.

We cannot discern these behavior patterns in the individual, or in short periods of time. The most intense scrutiny of an individual rabbit tells us

nothing of cycles. The cycle concept springs from a scrutiny of the mass through decades of history.

This raises the disquieting question: do human populations have behavior patterns of which we are unaware, but which we help to execute? Are mobs and wars, unrests and revolutions, cut of such cloth?

Many historians and philosophers persist in interpreting our mass behaviors as the collective result of individual acts of volition. The whole subject-matter of diplomacy assumes that the political group has the properties of an honorable person. On the other hand, some economists (5) see the whole of society as a plaything for processes, our knowledge of which is largely ex-post-facto.

It is reasonable to suppose that our social processes have a higher volitional content than those of the rabbit, but it is also reasonable to suppose that we contain patterns of which nothing is known because circumstance has never evoked them. We may have others the meaning of which we have misread.

This state of doubt about the fundamentals of human population behavior lends exceptional interest, and exceptional value, to the only available analogue: the higher animals. Errington (6), among others, has pointed out the cultural value of these animal analogues. For centuries this rich library of knowledge has been inaccessible to us because we did not know where or how to look for it. Ecology is now teaching us to search in animal populations for analogies to our own problems. The ability to perceive these, and to appraise them critically, is the woodcraft of the future.

To sum up, wildlife once fed us and shaped our culture. It still yields us pleasure for leisure hours, but we try to reap that pleasure by modern machinery and thus destroy part of its value. Reaping it by modern mentality would yield not only pleasure, but wisdom as well.

LITERATURE CITED

1. LEOPOLD, ALDO. 1933. The Conservation Ethic. Journ. Forestry, **31**: 634–643.
2. ROOSEVELT, THEODORE, T. S. VAN DYKE, D. G. ELLIOTT, and A. J. STONE. 1902. The Deer Family. New York, Grosset and Dunlap. (See especially the introduction by Roosevelt.)
3. WHITE, STEWART EDWARD. 1903. The Forest. New York, The Outlook Company.
4. LEOPOLD, ALDO. 1938. Conservation Esthetic. Bird Lore, **40**: 101–109.
5. BURNHAM, JAMES. 1941. The Managerial Revolution. New York, John Day Publishing Co.
6. ERRINGTON, PAUL L. 1940. On the Social Potentialities of Wildlife Management. Journ. Wildl. Mgt., **4**: 451–452.

THE STATE-SPORTSMAN-LANDOWNER TRIANGLE[1]

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The proper regulation of hunting and fishing is a topic upon which any man who ever drew a bead on a fleeting form or cast a fancy fly on the bubbling brook has expressed opinions in no uncertain terms. Local fish and game clubs many times have proposed resolutions only to see their good intentions go for naught. This failure is due in part to conflicting purposes within a group, in part to lack of definite policies clearly expressed by the state fish and game commissions, and in part to lack of supervision by game departments, but rarely to over-enthusiasm on the part of club members.

Each year organized sportsmen see themselves restricted by more and more regulations, of some of which they doubt the worth if not the validity, largely because they do not understand why they were adopted. A game department depends on revenues from the sale of licenses and to continue in office does a certain amount of restocking, brags about the capacity of fish hatcheries and game farms, puts much emphasis on law enforcement, but unfortunately neglects several other worthy phases. Sportsmen organize to realize their objectives, but often growl unceremoniously when farmers also organize. Many sportsman-farmer hunting cooperatives continue only a few years. Too many factors are involved to enumerate and discuss here, but if the legal aspects of acquiring game were better understood, more harmonious affiliations possibly might be achieved. When sportsmen fully realize the scope of activities of their fish and game departments, they will be more insistent that these departments equip themselves with proper personnel to carry out the many duties.

In the process of going hunting, trapping, or fishing, there are several generally accepted transactions between the hunter on the one hand and a state game department on the other, with the landowner taken for granted. It is self evident that a triangular relationship exists between the State, the hunter, and the landowner in the problems of filling the creel and the game bag. To clarify the issue, each of these groups is here recognized with respect to the ownership of game, the purchase of a license to acquire game, and the reduction of wild game to private ownership. The term "sportsman" connotes an ethical side to procurement and is not the proper word to indicate the mere act of acquiring or attempting to acquire game. The word "huntsman" is used here instead, and for want of a better term includes also fishermen and trappers.

[1] An excerpt, save for the opening and closing paragraphs, from a thesis prepared in 1936 under the late H. M. Wight, University of Michigan. His methods of teaching were such that I am uncertain as to which of the weaknesses enumerated here he first brought to my attention, or which recommendations he advocated for improving the farmer-sportsmen-State relationships. His skillful teaching methods made me aware of the strength and weakness of our present game system. The Boswellian element in this paper is indeed large.

First phase. GAME AS PROPERTY.

State is owner of wildlife.
Huntsman is consumer of wildlife.
Landowner is custodian of wildlife.

Second phase. TRANSFER OF PROPERTY IN GAME.

State gives consumer a chance to acquire said property by selling a license.
Huntsman is eligible to acquire said property after buying a license.
Landowner may, and sometimes does, block such transfer by making game areas inaccessible through prohibiting trespass.

Third phase. ACT OF ACQUIRING PROPERTY IN GAME.

State regulates the act of acquiring ownership in game by restrictions as to the kinds, time, places, numbers, and manner of taking.
Huntsman's success in acquirement depends upon:
a. Abundance of game,
b. Availability of game areas, and
c. Skill and knowledge of hunting, fishing, or trapping.
Landowner influences the act of acquirement by
a. Directly controlling the availability of areas, and
b. Indirectly controlling the abundance of game species.

The weaknesses in this triangular system are many. Several are briefly enumerated below, followed by recommendations for overcoming them.

1. The State deals directly with the consumer in selling him a license, usually without providing him with sufficient hunting areas. This transaction ignores the position of the landowner.

2. The State is unable to guarantee availability of game to any particular person.

3. There are few seasonal bag limits. Hence some hunters may acquire far more than their proportionate share of game, thus depriving others of the chance to get their share. A seasonal bag limit for waterfowl and small game would be very difficult to enforce, except in regulated areas.

4. Once an area is opened to hunting, the State does not guard against the chance of extermination of species within the time that the area is legally open.

5. The State does not increase game abundance materially, if at all, by any positive action. (Fish and game plantings usually afford only temporary relief.)

6. The landowner receives no remuneration for his efforts toward preservation of wildlife.

7. None of these three parties gives enough attention to the direct requirements of game species. Sporadic efforts are made to decrease mortality rates, but none is made to increase the average annual birth rate or survival at various stages in the life of the animal.

8. The State in selling licenses where there is no restriction on a seasonal bag limit often sells the right to take more game than exists; if every person doubled his annual take, there would soon be a near extirpation of various species. The State blindly trusts to the law of supply and demand to preserve animals when they are scarce.

These weaknesses are the result of a system which is like Topsy—it just grew. A half century ago, it was the exceptional state game department that did not officially believe in the Legend of Inexhaustibility. Hence, when the day of reckoning arrived, the reform was, and still is, largely a patchwork—a reduction in bag limits here, shorter hours there, closed feeder streams somewhere else. There was no appraisal of

the situation in its entirety, followed by fitting the reforms to the needs.

To cut this Gordian knot of "who does what" in game affairs, I propose, for what they are worth, the following matters relative to small game, furbearers, and fishes. I suggest (Point 9) that the hunter pay the farmers or farmer organizations directly for the privilege of hunting on their land. Some may think it better to add 25 or 50 cents to the license fee and have the State pay the farmer, but most hunters do not want to pay the additional money unless they get direct benefits. Therefore, let the hunter pay the man who has managed his own area to provide better than average shooting.

The alternative is never to pay the landowner. If so, why should he do anything to favor the game? There are far too many unmanaged or even mismanaged areas today, and an appeal to the profit side of a farmer's venture in true game management is one way to improve the food and cover for game.

Here are thirteen points in which the State should be the leader in game improvement work and the referee in farmer-sportsman arguments. The points are stated affirmatively, not to be dogmatic, but to make the issues clear cut.

1. The State must recognize the landowner as the custodian of game.

2. There must be flexible game laws available to a technically trained commission and administered in the field by wildlife technicians.

3. The State must proclaim definite seasonal limits for many species and daily time limits on the hunting of upland game birds, that is, the opening or closing hour or both for each day.

4. Every county will have two or more separate large areas (of 2,000 acres or more) managed for its more important wildlife species. If of farm lands, these areas would need to be leased.

5. These areas will be managed or supervised by wildlife technicians so as to increase the population of one or more species, and also to afford more sport in the act of procurement (i.e. more difficulty in shooting and a reasonable hour-per-kill ratio, such as an hour required on the average to shoot each pheasant).

6. The State must advise the landowner on factors of game management. This requires a manager-warden type of field man who is a trained game technician. A few states are gingerly beginning in this respect.

7. The State will supply the farmer at cost with seeds or seedlings for improvements such as food patches and winter escape coverts and must have one or more nurseries to supply these materials; surpluses will be sold to others at retail prices.

8. The State will advise and act as mediator whenever necessary in organizing farmers and hunters in separate cooperative clubs and in urging the leaders of each group to meet the other and handle their wants and grievances between themselves.

9. The State must foster and supervise a means whereby the hunter directly reimburses the farmer or farmer organization for providing better than ordinary hunting. This system must be flexible and responsive to the laws of supply and demand, but not too dependent upon them. The purpose is to stimulate the farmer to make a better

environment for game which, on inincreasing, brings more hunters to his place and thus increases his revenue. The landowner, on his part, will invest at least half of the profit in improving the habitat for wildlife.

10. Half of all license money received from hunting each class of game will be expended in the county for which it is designated to promote game projects and to buy or lease land for game propagation. In other words, half of the money is to be invested in maintaining or enlarging the capital on areas in proportion to the demand; the other half is used to meet current expenses of the game department.

11. Areas of hunting must be handled on their individual merits. All areas will be opened to hunting on a certain date, but each will be closed as soon as the previously allotted kill has been removed. The huntsmen must understand that if an area is over-shot, over-trapped, or over-fished, it will be either closed for one or more seasons or the kill will be reduced until the game supply is back to normal.

12. For ease in distribution of game funds according to source, and in checking on the amount of game taken and the success ratio of huntsmen there should be five separate licenses: one each for fishing, trapping, hunting big game, waterfowl, and upland game.

13. The state game department must establish information and research divisions. The latter need not be strictly in the department as it can draw help from various Federal agencies, and the colleges and state universities. The information division would use movies, slides, specimens, exhibits, and newspaper releases to keep the hunters, trappers, and fishermen posted on current developments.

Many state game departments are doing some of these things now. On the information side many have splendid bulletins to inform and educate their sportsmen. If so, how well is the average license buyer posted on the many activities of his game and fish department?

Now that additional funds are available to the states under the federal aid grants for wildlife restoration (Pittman-Robertson Act), there is greater opportunity for research, more intensive and extensive administration, and for more land acquisition, all for better game, fur, and bird production than heretofore achieved. A bill now in Congress would revert funds from excise taxes on fishing tackle and supplies to improve inland fishing resources. Preceding the increase of funds there was the instruction offered in various schools in wildlife management. Today nearly two score of institutions teach the basic and essential elements of waterfowl development, big game management, farm-game management and many other phases, thus training men today to be tomorrow's leaders.

If sportsmen will encourage their State agencies to provide the trained leadership which proper management of wildlife resource demands, then amalgamation of funds, wise leadership, trained field men, and cooperation of sportsmen and landowner will do wonders to restore shooting, trapping, and fishing. This, however, requires cooperation all along the line.

USE OF BAG RECORDS OF BIG GAME TO DETERMINE SEX RATIOS AND POPULATION DENSITIES

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In the scientific management of big game a knowledge of the existing population densities and sex ratios is of greatest importance but very difficult to obtain. At present tedious census methods are the only approach to these problems. This paper describes a means to determine what is *not* the existing population density or sex ratio, and thus limit the possibilities to a narrow range. It requires a knowledge of the number of bucks killed within a known acreage. If either the population density or the sex ratio is already known, the range of the other and unknown factor can be narrowed to a greater degree.

To demonstrate our method we shall use as a definite example the "Summary of Records of Shooting Preserves Reporting Deer Killed" by Sanders (Journ. Wildl. Mgt., 6: 187, 1941). He records a total kill of 5,617 bucks on 984,097 acres of shooting preserves, an average of one to 172 acres, in four Texas counties—Kerr, Llano, Gillespie, and Mason—where the sportsmen believe that the range is greatly overpopulated and the sex ratio of deer is seriously out of balance. It is contended that there are 10 to 50 does for each buck on the range, but the wildest of these claims can definitely be disproved.

The known factor is one buck killed for every 172 acres; the sex ratio, population density, and percentage of bucks killed by sportsmen are unknown. To widen our knowledge of either sex ratio or population density a series of hypothetical figures is established for one or the other factor. It is immaterial which is used. This is demonstrated in Table 1 where population density is treated as the unknown factor and hypothetical figures are used for the sex ratio. Instead of using all possible hypothetical sex ratios we use units of 5, from 5 to 50.

Hypothetical sex ratios were used ranging from 1:1 to an arbitrary 1:50. If the sex ratio were 1 buck to 50 does, there would be an average of 51 deer on each 172 acres (1 buck+50 does) or one per 3.4 acres (bottom row, Table 1). This would hold true only if every buck had been shot, an absurd supposition since male fawns and unpronged bucks were not hunted. Moreover, some legal bucks survived the hunting season, and others died in the wild without being recorded. It is reasonably certain that at least one-half of the buck population was not shot by hunters, perhaps not even one-third. In Table 1 are listed the possibilities if one-half, one-third, and one-fourth of the entire buck population had been killed by hunters. We assume that half of them were so killed. The chart shows that it would be nearly impossible to have the sex ratio more unbalanced than 1:20, which would mean the presence of 42 deer, or one per 4.1 acres.

Such a population density is possible in restricted localities, but is unreasonable to expect on the almost one million acres under consideration as livestock also graze the range (the grazing density in the four counties between

10.06 and 7.18 acres per animal unit). Various ranges in the United States with one deer to 7 acres are reported as overpopulated. Such high populations reduce forage to the point of extermination. It is possible, but not probable, in areas where bucks and no does have been hunted legally for a number of years, we can with certainty state that the area contains more than two deer or one to 86 acres. Furthermore, we can reasonably assume that hunters did not

Table 1.—POSSIBLE POPULATION DENSITIES OF DEER WITH HYPOTHETICAL FIGURES FOR THE SEX RATIO. PREMISE: ONE BUCK KILLED PER 172 ACRES. (*Italic numbers in parentheses give acres per deer.*)

Bucks Killed	Population of deer to 172 acres			
	All	One-half	One-third	One-fourth
Bucks per 172 acres	1	2	3	4
Sex ratio				
1: 1	2 (*86*)	4 (*43*)	6 (*28.5*)	8 (*21.5*)
1: 2	3 (*57.3*)	6 (*28.6*)	9 (*19*)	12 (*14.3*)
1: 3	4 (*43*)	8 (*21.5*)	12 (*14.2*)	16 (*10.7*)
1: 4	5 (*34.4*)	10 (*17.2*)	15 (*11.4*)	20 (*8.6*)
1: 5	6 (*28.6*)	12 (*14.3*)	18 (*9.5*)	24 (*7.1*)
1:10	11 (*15.6*)	22 (*7.8*)	33 (*5.1*)	44 (*3.9*)
1:15	16 (*10.7*)	32 (*5.3*)	48 (*3.5*)	64 (*2.6*)
1:20	21 (*8.2*)	42 (*4.1*)	63 (*2.7*)	84 (*2.0*)
1:25	26 (*6.6*)	52 (*3.3*)	78 (*2.2*)	104 (*1.6*)
1:30	31 (*5.5*)	62 (*2.7*)	93 (*1.8*)	124 (*1.4*)
1:35	36 (*4.8*)	72 (*2.4*)	108 (*1.6*)	144 (*1.2*)
1:40	41 (*4.2*)	82 (*2.1*)	123 (*1.4*)	164 (*1.0*)
1:45	46 (*3.8*)	92 (*1.9*)	138 (*1.2*)	184 (*0.9*)
1:50	51 (*3.4*)	102 (*1.7*)	153 (*1.1*)	204 (*0.8*)

that the 172 acres contain 32 deer, or one to every 5.3 acres, so the table has reached the limit of its usefulness. The sex ratio, consequently, must lie somewhere between 1:1 and 1:20.

The method can also be used to obtain more accurate estimates of population densities. Since there is no reason to believe that the sex ratio could be 1:1

Table 2.—ESTIMATED SEX RATIO OF DEER POPULATION IF ACRES PER DEER KILLED AND POPULATION DENSITY ARE KNOWN. (*Assumed population 12 deer, one to 6.58 acres.*)

Assumed number of bucks killed	*Buck population*	*Sex ratio*
all	1 to 79 acres	1:11
one-half	1 to 39 acres	1:5
one-third	1 to 26 acres	1:3
one-fourth	1 to 19 acres	1:2

kill one-half of the bucks, and that the population is not less than four, or one deer to 43 acres. (See first figures, second and third column of Table 1.)

If per chance a biologist could add another known factor to the table, its usefulness would be very much increased. On page 188 of Sanders' article, there is a tabular "*Summary of records of shooting preserves on which the deer killed was one or more per 100 acres and calculations of the number of deer for unit herds.*" This provides two known factors, the acres per buck killed (1 to 79 acres) and the population density (12 deer or 1 to 6.58 acres) based on "acres per deer calculated for herd of 12 deer per buck killed." Had he proceeded

with the statistical method here described he could have estimated the sex ratio as in our Table 2. (It must be kept in mind that the purpose of this paper is not to determine sex ratios or population densities in West Texas, but merely to demonstrate a technique.)

He would thus have established that the sex ratio must be between 1:1 and 1:11. Since hunters did not kill all the bucks, he could with reasonable assurance say that the sex ratio lies somewhere between 1:5 and 1:2.

CONCLUSIONS

1. More practicable and simpler wildlife census methods are needed.

2. Where accurate records of the kill of big game on a known acreage are kept, it is possible by statistical methods to show the limits for sex ratio and population density, and to disprove absurd estimates.

3. The usefulness of this method is limited; its value increases in proportion to the completeness of the field data.

WINTER FOOD PRODUCTIVITY OF AGRICULTURAL LAND FOR SEED-EATING BIRDS AND MAMMALS

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The importance of some common weeds as food for wintering animals has been amply demonstrated, but little has been done to show the amounts and availability of these foods on agricultural land. During the fall and winter of 1940–41, an investigation on the latter topic was carried on at the Rose Lake Wildlife Experiment Station of the Michigan Department of Conservation in Clinton County, Michigan. It was planned to learn the productivity of a sample of farmland in winter food for granivorous species, the length of time the food remains available, the relationship of soil fertility to weed production, the weed species most important as food, the value of farm crop residues, and the extent to which the foods are used by various animals.

WEED SEEDS

Quantitive collections of seeds were made by clipping squared meter quadrats at random every month during the winter in fields representing the common soil types and devoted to various farm crops. From one to five samples were taken in each field depending on its size and the uniformity of the weed stand. Only the seeds on stems were collected. The samples were cut, placed in tightly woven grain sacks, dried, and threshed, and the seeds sorted by species. Each sample was then weighed and the production in pounds per acre was calculated. The fields sampled included stubble of corn, oat, and wheat, standing corn, mechanically-picked cornfields, fallow food patches, and gardens.

The analyses showed that 10 weed species were sufficiently abundant to be considered important, approximately in order of value as follows: Lesser ragweed (*Ambrosia elatior*), green foxtail (*Setaria*

viridis), lambsquarters (*Chenopodium album*), yellow foxtail (*Setaria glauca*), black bindweed (*Polygonum convolvulus*), smartweed (*Polygonum persicaria*), barnyard grass (*Echinochloa crusgalli*), finger grasses (*Digitaria ischaemum* and *D. sanguinalis*), old witch grass (*Panicum capillare*), and pigweeds (*Amaranthus retroflexus* and *A. graecizans*). item, and were more important than all the cultivated grains combined.

Following ragweed in order of occurrence was green foxtail, which persisted suprisingly well into March. Yellow foxtail, on the other hand, was relatively plentiful as late as November, then shattered and disappeared almost entirely from the samples. The seeds of

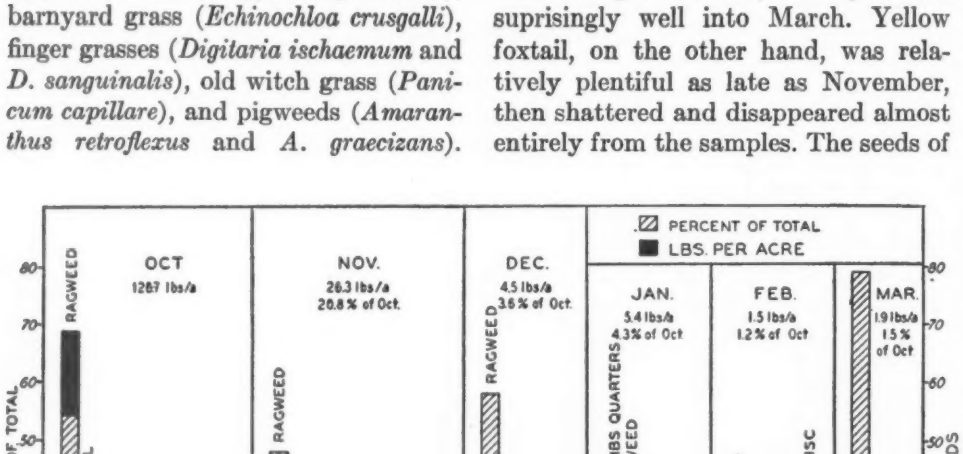

Fig. 1. Quantities of common weed seeds available by months.

Their relative abundance during the six-month period is shown in Figure 1.

The relative abundance of ragweed was strikingly apparent; in some cases it comprised 50 per cent or more of the monthly totals of all species available. Of possibly greater significance than abundance was its availability in quantity throughout the winter. An indication of its importance as a food producer for pheasants was obtained from an analysis of crops collected in October and November during the 1940 hunting season. Its achenes were the leading both yellow and green foxtails are excellent bird food. The achenes of black bindweed and smartweed, although not abundant, remained available through most of the winter, and were often found in the crops of pheasant. The remaining species named were present in lesser quantities and probably served best in providing food for songbirds.

Food production for the several habitats varied in both the quantity and species of weeds produced. Fallow gardens provided more wildlife foods

Table 1.—PRODUCTION OF WEED SEED AND SEASONAL AVAILABILITY BY HABITATS.

Habitat	Pounds of Weed Seeds per Acre					
	Oct.	Nov.	Dec.	Jan.	Feb.	March
Fallow Garden	456.8	250.6	31.6	5.1	18.3	13.0
Wheat Stubble	211.5	39.4	8.2	3.1	1.5	0.4
Standing Corn[1]	162.4	23.9	0.8	7.7	0.2	9.2
Lespedeza[2]	148.8	8.3	3.6	0.4	1.3	0.6
Oat Stubble	111.1	25.6	10.8	2.2	2.6	1.0
Corn Stubble[3]	109.6	35.5	1.9	18.2	0.6	1.6
Standing Corn and Food Patch[4]	53.1	17.8	4.8	3.6	2.4	0.3
Fallow Food Patch	—	13.0	2.7	2.6	0.6	0.5

[1] The rapid decrease possibly indicates more use by wildlife.
[2] Lespedeza did not thrive on the poor Coloma sand and ragweed volunteered.
[3] Includes fields cut both by hand and by binder.
[4] On poor soils: Coloma sand and Oshtemo sandy loam.

than any other type of habitat (Table 1); they were on Newago and Miami loams, well fertilized and drained. In October, the yield averaged 456.8 pounds of weed seeds per acre, 73 per cent being lambsquarters and pigweeds. This abundance seemed especially attractive to songbirds such as juncos, tree sparrows, and goldfinches.

Wheat stubble fields were also highly productive, with ragweed predominating. Two fields averaged 211.5 pounds of weed seeds per acre in October, 97 per cent being ragweed. Leedy (1939), in Wood County, Ohio, found ragweed to predominate in wheat stubble, averaging 85.9 pounds per acre in 15 fields during October. It is evident that plowing under wheat stubble in the fall deprives wildlife of an excellent source of winter food, and needless to say, also accelerates soil erosion. Leedy found smartweed most abundant in moist cornfields, and foxtail grass in the drier ones, as did the writer.

Soil fertility probably is equally as important as type of habitat in determining the productivity and kinds of weeds. Other factors being equal, the quantity of weed seeds produced per acre varies directly with soil fertility (Table 2). Newago loam was about four times as productive as the poorer Coloma sand, yielding in October, 307.7 pounds as compared with 78.7 pounds on the sand. Sandy soils are relatively unproductive and generally the species they produce are of little value to wildlife. For instance, the sandbur is typical of local sandy soils, and is used to some extent by pheasants but cannot compare with ragweed in production of wildlife food. Ragweed, pigweeds, lambsquarters, all were more abundant on the better soils.

Table 2.—WEED SEED PRODUCTIVITY AND AVAILABILITY BY SOIL TYPES.

Soil type and habitat	*Pounds per Acre*	
	Oct.	*Mar.*
Miami Loam. Oat stubble, two fallow gardens	329.8	8.9
Newago Loam. Corn stubble	307.7	1.0
Bellfontaine Sandy Loam. Standing corn, corn stubble, two food patches	202.3	0.5
Crosby Loam. Wheat stubble	156.0	0.2
Conover Loam. Wheat, oat, and corn stubble, standing corn	154.9	5.5
Coloma Sand. Lespedeza seeding, corn stubble, standing corn, food patch	78.7	0.3
Oshtemo Sandy Loam. Corn stubble and food patch	64.8	0.25

The intensity of crop cultivation is also a factor in limiting weed seed production. The more thoroughly a field is cultivated the fewer weeds it will produce, particularly when cultivation is continued late in the summer. Wright (1941) states "the quantity of weed foods available for game birds is governed by the amount of land in cultivation and the practices of farm management, as the extent of 'clean farming,' fall plowing, etc."

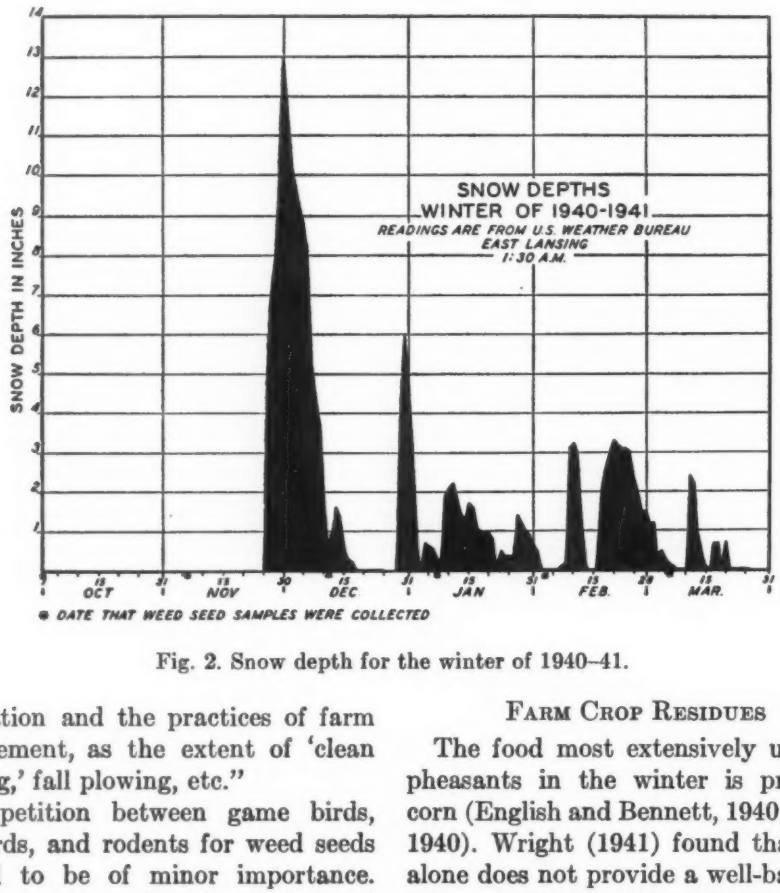

Fig. 2. Snow depth for the winter of 1940–41.

Competition between game birds, songbirds, and rodents for weed seeds seemed to be of minor importance. Seeds were generally abundant, and usually available because of the mild and open winter (Fig. 2). Allen (1938) has shown that the intensity of competition between wildlife species for winter foods is correlated with depth of snow. Many seeds shaken from the stems fell on snow-free spots of ground, and songbirds frequently fed on such seeds. A small series of juncos and tree sparrows was collected and found to have eaten mainly the small seeds of witch grass, pigweeds, and lambsquarters, and lesser amounts of ragweed achenes.

FARM CROP RESIDUES

The food most extensively used by pheasants in the winter is probably corn (English and Bennett, 1940; Fried, 1940). Wright (1941) found that corn alone does not provide a well-balanced ration and that weed seeds are dietetically superior to cereals. McAtee (1937) makes it clear that corn is deficient in proteins and their amino-acids, in calcium, and vitamins A and B, and it is lacking in vitamins C and D. Despite

these deficiencies, corn is important as a winter food of game animals.

Three mechanically-picked cornfields were sampled for waste corn immediately after harvest; an average of 6.7 bushels per acre (at 56 pounds per bushel of shelled corn) had been left by the pickers. All of this grain, however, was not long available to wildlife. Local farmers agreed that ordinarily most of it would be consumed by cattle and hogs, but stock was turned into only two of the fields. The third was used extensively by rabbits, pheasants, and fox squirrels during most of the winter, even when they were forced to dig through several inches of snow. For a short time in late November a flock of about a thousand black and gray mallards also fed on the corn. The available grain thereby diminished from 10.1 bushels per acre on November 8 to 7.7 bushels per acre by December 19.

Wheat and oats shattered and left in the field during harvest were measured in 1941 in two oat and two wheat fields cut with a tractor-drawn binder. Waste wheat averaged 2.4, and oats 3.5, bushels per acre (60 pounds per bushel for wheat and 32 pounds per bushel for oats). The principal use of these grains was by starlings and blackbirds. Pheasants also fed upon them and on September 1 about 45 black and gray mallards were feeding in one wheat field.

MAST

Mast production by the common nut trees was measured in October and November. These included: white oak (*Quercus alba*), black oak (*Q. velutina*), red oak (*Q. borealis maxima*), beech (*Fagus grandifolia*), shagbark hickory (*Carya ovata*), small-fruited hickory (*C. ovalis*), walnut (*Juglans nigra*), and butternut (*J. cinerea*). The productivity of hickories varied markedly; trees in woodlots yielded practically nothing and isolated trees only a fair crop. Three small-fruited hickories averaged 7.3 quarts of shelled nuts each, three shagbark hickories 1.2 quarts per tree, and ten walnut trees 56 quarts of unshelled nuts each. Oak and beech trees failed to produce. These data on mast were provided by Joseph P. Linduska of the Rose Lake staff. The fact that the mast crop for 1940 was very nearly a failure seemed not to have had any material effect on the fox squirrels; those examined during the winter were normal in weight and condition, possibly because of the availability of shocked corn.

SUMMARY

1. Foods on an area of agricultural land in Michigan were sufficient to supply the winter needs of the wildlife population.
2. Wheat stubble fields were especially productive of ragweed seeds, averaging 205 pounds per acre in October.
3. Soil fertility and weed seed production are directly related.
4. Because of the adequate and available supply of weed seeds and grains throughout the winter, competition between game and other species was of minor consequence.
5. Corn is a major wildlife food. Cornfields picked with a mechanical picker yielded, after harvest, an average of 6.7 bushels of shelled corn per acre. Most of this was salvaged by livestock; the remainder was used by wildlife.

6. Wheat fields cut with a tractor-drawn binder yielded 2.4 bushels of waste grain per acre and oat fields 3.5 bushels per acre. These were used mainly by starlings and blackbirds but to some extent by pheasants and ducks.
7. The mast crop in 1940 was almost a total failure, yet fox squirrels survived the winter in good condition, probably because of an available supply of shocked corn.

LITERATURE CITED

ALLEN, DURWARD L. 1938. Ecological studies on the vertebrate fauna of a 500-acre farm in Kalamazoo County, Michigan. Ecological Monographs, 8: 347–436.

ENGLISH, P. F. AND LOGAN J. BENNETT. 1940. November foods of ring-necked pheasants and bobwhites. Pennsylvania Game News, 10(1): 8–9, 29.

FRIED, LOUIS A. 1940. The food habits of the ring-necked pheasant in Minnesota. Journ. Wildl. Mgt., 4: 27–36.

LEEDY, DANIEL L. 1939. Some land use factors related to pheasant production. N. Amer. Wildl. Conf., Trans. 4: 525–533.

MCATEE, W. L. 1937. [Special Article.] Wildlife Review, No. 9: 36–37.

WRIGHT, THOMAS, JR. 1941. A study of the fall food supply of the ring-necked pheasant and the bobwhite quail in Washington County, Rhode Island. Journ. Wildl. Mgt., 5: 279–296.

POPULATION DENSITY OF BROWN TROUT IN CRYSTAL CREEK, NEW YORK, 1939–41

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In recent years there have been several investigations to determine the most efficient methods of stocking trout as measured by the number surviving after a specified period of time. Information on the survival of fish of various sizes and planted under different conditions is one criterion for selecting the most efficient stocking policy. The stocking table of G. C. Embody (1926), designed as a preliminary estimate of the survival rates for various sizes of trout in certain types of streams, has been accepted by many as a finished product and few attempts have been made to check its reliability. Recent data suggest that the table may be faulty or incomplete for some situations, and attempts are being made to check its accuracy by practical experiments.

One such project is being carried on at Crystal Creek, New York State's experimental trout stream.[1] The survival of different plantings, made to Embody's specifications, is being determined to supplement the table and to

[1] The author is indebted to D. G. Pasko, A. C. Petty, R. G. Zilliox, C. Heacox, S. L. Crump, and J. J. Porter of the Crystal Creek personnel for collecting many of the data; to Sumner M. Cowden and Oliver R. Kingsbury of the New York State Bureau of Fish Culture and Dr. Emmeline Moore of the State Bureau of Biological Survey, under whose direction the work was carried out; and to Dr. C. McC. Mottley and D. R. Embody of Cornell University for aid in preparing the manuscript.

learn the most economical number and size of brown trout (*Salmo trutta*) and the time and method of planting needed to produce satisfactory fishing.

There are two recognized methods of obtaining data to evaluate the effects of fish planting. The creel census provides an estimate of the yield of legal-sized fish to the angler, but has several disadvantages, as only legal-sized fish are directly observed, and little information is afforded where the fishing pressure is relatively light, as in Crystal Creek. Where little information is afforded by the creel census, the differences in yield must be large to be judged as significant. The second method is to estimate the population density by direct count of those remaining after some specified period of time. This has an advantage in that plantings of both fingerlings and legal-sized fish can be observed directly. Such an estimate usually involves sampling, as only short sections of stream can be studied in one operation.

Various techniques have been used to estimate the densities of fishes in streams, including (1) seining (Shetter and Hazzard, 1939; Trippensee, 1937; Greeley and Bishop, 1933); (2) diverting water from the stream (G. C. Embody, 1929); (3) pumping sections dry (Needham and Rayner, 1939); and (4) the use of various poisons to produce temporary or permanent loss of equilibrium in fishes (D. R. Embody, 1940; Leonard, 1939; Smith, 1940, 1941; Hoover and Morrill, 1938).

Table 1.—NUMBERS OF WILD BROWN TROUT TAKEN IN SECTIONS OF CRYSTAL CREEK, NEW YORK, 1939–41.

Stream section		Total length (feet)	Fingerlings			Sub-legals			Legals		
			1939	1940	1941	1939	1940	1941	1939	1940	1941
Flat water sections	1	283	12	13	7	3	3	0	4	3	7
	2	221	9	8	4	5	7	4	9	8	3
	3	225	5	11	4	4	10	6	9	3	2
	4	253	16	17	8	4	2	3	4	5	2
	5	215	6	2	7	0	1	0	3	2	2
	6	205	6	2	0	0	0	1	0	1	0
	7	300	12	3	3	1	5	2	6	7	4
	8	193	2	12	4	0	1	1	2	3	1
Riff water sections	1	203	11	14	15	0	0	0	1	1	0
	2	98	6	3	15	2	7	5	4	4	1
	3	204	5	9	11	14	2	6	4	3	2
	4	204	21	11	26	11	14	7	3	8	1
	5	184	10	14	2	14	19	12	5	9	0

An additional means of removing fish from streams, by electrical shocking, has recently been developed. Preliminary studies indicate that this is more efficient than seining, but the method has not been critically appraised. A preliminary test to estimate the stock of trout was made in a three-year study at Crystal Creek.

Thirteen sections of stream averaging 215 feet in length were selected; these 2,788 feet included about 12.7 per cent of the total stream length. Eight were of a slow or "flat" water type, and the other five of fast or "riff" water. The distribution of riff and flat water sections was roughly propor-

tional to the total amount of each type in the whole stream. The density of wild brown trout in each section was estimated at the close of the fishing seasons of 1939, 1940, and 1941.

Operations were conducted on all of these sections following the procedure recommended for the electrical shocking method described by Haskell (1940) and Haskell and Zilliox (1941). The data accumulated, are shown in Table 1. The total length was recorded for each wild brown trout captured and three classes were recognized: *fingerlings*, or young of the year; *sub-legals*, or all between fingerlings and "legals"; *legals*, or all trout 17.8 cm. in total length or larger. The dividing line between fingerling and sub-legal sizes was not exact, but little confusion resulted because the former could be distinguished readily.

Table 2.—REDUCED DATA FOR THE ANALYSIS OF VARIANCE AND TESTS OF SIGNIFICANCE.

Source of variation	D.F.	Sum of squares	Mean square	F value	D.F.	Significance
Total	116	121.41				
Years	2	4.080	2.04	5.009	2,48	Significant
Classes	2	25.37	12.68	10.773	2,24	High
Sections	12	35.51	2.959	2.514	12,24	Significant
Years × Classes	4	1,102	.2755	.6764	4,48	None
Years × Sections	24	7.550	.3146	.7724	24,48	None
Classes × Sections	24	28.25	1.177	2.890	24,48	High
Years × Classes × Sections	48	19.55	.4073			

THE PROBLEMS AND POSSIBLE SOLUTION

In using these data to estimate the population densities, it is necessary to determine how the number of trout fluctuates with various factors such as: (1) The years (1939, 1940, and 1941); (2) the individual stream sections; (3) the riff and flat water sections; and (4) the three size classes of trout. The hypothesis to test is that no differences associated with these factors are large enough to be considered significant.

The Design. The analysis of variance (Fisher, 1938) provides tests of significance for groups of data similar to these. Variations associated with years, water types, classes of trout, and lengths of sections can be segregated, compared, and judged as to significance by the F-test (Snedecor, 1940). To avoid correlation between mean and variance, all values have been transformed to the square root of the original number plus 0.5. The 5 per cent level will be taken as the minimum point for significance.

Tests of Significance. The reduced data and the tests of significance are shown in Table 2. An F value of 5.009 indicates that the population density was different in the various years. To determine in which of the three years the variation was significant, the numbers of all fish per section in 1939 and

1940 were compared. There was no significant difference in the totals of all three classes of fish between 1939 (17.9 trout per section) and 1940 (19.0), but between 1939 (17.9) and 1941 (13.7) the difference was highly significant. Inasmuch as 1939 and 1940 were similar, it may be inferred that 1941 was also different from 1940 (Table 3).

Thus there was a marked decrease in the total number of trout in the 13 sections in 1941, from 1939 and 1940. To determine if all or only one or two of the classes of fish contributed to this decrease, the average numbers of fingerlings, sub-legals, and legals were compared separately, for 1939 and 1941. There was no significant difference between the mean number of fingerlings per section in 1939 (9.31) and 1941 (8.15), or between the mean number of sub-legal fish in 1939 (4.46) and in 1941 (3.62). The difference between the numbers of legal-sized trout, however, was highly significant; The average dropped from 4.15 per section in 1939 to only 1.92 in 1941. No significant differences were found between the densities of either fingerlings, sub-legals or legals in the three years.

Table 3.—AVERAGE NUMBER OF FISH BY SIZE PER SECTION.

Year	*Fingerlings*	*Sub-legals*	*Legals*	*All classes*
1939	9.31	4.46	4.15	17.9
1940	9.15	5.46	4.38	19.0
1941	8.15	3.62	1.92	13.7
Averages	8.87	4.51	3.49	16.9

As between the 13 sections, an F-value of 2.5 with 12 and 24 degrees of freedom indicated a significant difference. A comparison of the average number of fish per year in each is shown in Table 4. The sections differ in length (98 to 300 feet), so it might be supposed that the numbers of fish would be associated with variations in length of the sections. To test this a correlation coefficient (r) was estimated between the length of the sections in feet and the number of sub-legal and legal fish present in each section in the average year. A value of .0059 for r is not significant; neither is a value of .0497 for the correlation between length of section and the number of fingerling trout per section.

Table 4.—AVERAGE NUMBER OF TROUT PER YEAR IN THE 13 SECTIONS.

Stream section	*Fingerlings*	*Sub-legals*	*Legals*	*All classes*
1	10.70	2.00	4.67	17.3
2	7.00	5.33	6.67	19.0
3	6.67	6.67	4.67	18.0
4	13.70	3.00	3.67	20.3
5	5.00	.33	2.33	7.7
6	2.67	.33	.33	3.3
7	6.00	2.67	5.67	14.3
8	6.00	.67	2.00	8.7
1	13.30	.00	.67	14.0
2	8.00	4.67	3.00	15.7
3	8.33	7.33	3.00	18.7
4	19.30	10.70	4.00	34.0
5	8.67	15.00	4.67	28.3
Average, all sections	8.87	4.51	3.49	16.9

Water types. To learn whether the density of trout was different in riff and flat waters the total trout of all three classes in the average year per section of the two types was compared; riff sections contained 22.1, a significantly greater density of trout, than the 13.6 in flat water.

There was no significant difference between the average number of fingerlings in the riff (11.5) and in flat-water sections (7.21), or between the number of legal fish—riff (3.07) and flat water (3.75); however, there was a significant difference in the average number of sub-

legal fish—riff (7.53) and flat water (2.62) per section (Table 5).

Classes of fish. Considering the relative densities of fingerlings, sub-legals, and legals in all sections in the average year, the numbers of sub-legal and legal fish was practically the same per section (4.51 sub-legals, 3.49 legals). The number of fingerlings per average section (8.87) was, however, significantly greater than either the number of sub-legals, or of legals per section (Table 5).

Table 5.—AVERAGE NUMBER OF FISH PER YEAR BY KIND OF WATER.

	Fingerlings	*Sub-legals*	*Legals*	*All trout*
Riff	11.5	7.53	3.07	22.1
Flat	7.21	2.62	3.75	13.6
Both	8.87	4.51	3.49	16.9

A single section studied in any year produced about 0.137 units of information for the estimation of the density of any class of trout. About 7 sections would thus produce one unit of information, which is acceptable for the solution of most agricultural production problems.

CONCLUSIONS

This study seems to warrant the following conclusions:

1. A significant difference was found in the numbers of wild brown trout captured in the sample sections of Crystal Creek, New York, in various years. In 1939 and 1940 the population density was practically the same for all three size classes of fingerling, sub-legal and legal, but in 1941 was significantly lower, resulting from a drop in the population of legal trout. The spawning run of legal-sized trout in the autumn of 1941 was considerably less than in 1940, thus supporting the findings as to population.

2. Between the 13 sections of the creek the variation was greater than expected on a chance basis; this was not associated with the lengths of the sections and probably was due to some preference of trout difficult to evaluate. Possibly the differences in population density were associated with differences in the total area or volume of water per section.

3. Between the riff and flat water sections there was a significant difference in population density, with more sub-legal trout in the riff sections. There were no significant differences in the numbers of either fingerlings or legal trout in riff and flat water.

4. The relative numbers of legal and sub-legal fish were practically identical, but the density of fingerling trout was significantly greater as might be expected.

5. The method which is described would appear to be a relatively precise one for the estimation of the density of trout in this stream on the basis of the variability of the 13 sample sections. Seven sections would produce about one unit of information in any year, adequate to detect a difference of 10 per cent. Lesser differences in population density are not likely to be important in testing the effect of various stocking methods, so the technique is deemed satisfactory for obtaining data to evaluate the survival of trout in this stream.

LITERATURE CITED

EMBODY, D. R. 1940. A method of estimating the number of fish in a given section of stream. Am. Fish. Soc. Trans. (1939), 69: 231–236.

EMBODY, G. C. 1929. Stocking policy for the streams, lakes and ponds of the Erie-

Niagara Watershed, exclusive of Lake Erie. New York State Conserv. Dept., Ann. Rept. (1928) **18**, Supplement: 23–24.

FISHER, R. A. 1936. Statistical methods for research workers. Edinburgh, Oliver and Boyd, 339 pp.

1937. The design of experiments. Edinburgh, Oliver and Boyd. 260 pp.

GREELEY, JR., R. and S. C. BISHOP. 1933. Fishes of the Upper Hudson Watershed with annotated list. New York State Conserv. Dept., Ann. Rept. (1932) **22**, Supplement: 64–101.

HASKELL, D. C. 1940. An electrical method of collecting fish. Am. Fish. Soc., Trans. (1939), **69**: 210–215.

HASKELL, D. C. and R. G. ZILLIOX. 1941. Further developments of the electrical method of collecting fish. Am. Fish. Soc., Trans. (1940), **70**: 404–409.

HOOVER, E. E. and G. W. MORRILL, JR. 1938. Autecology of brook trout (*Salvelinus fontinalis*) in two primitive streams of Northern New Hampshire. New Hampshire Fish and Game Dept., Tech. Circ. **2**: 1–22.

LEONARD, J. W. 1939. Notes on the use of derris as a fish poison. Amer. Fish. Soc., Trans. (1938), **68**: 269–279.

NEEDHAM, P. R. and H. JOHN RAYNER. 1939. The experimental stream, a method for study of trout planting problems. Copeia, **1939**: 31–38.

SHETTER, D. S. and A. S. HAZZARD. 1939. Species composition by age groups and stability of fish populations in sections of three Michigan trout streams during the summer of 1937. Am. Fish. Soc., Trans. (1938), **68**: 281–302.

SMITH, M. W. 1940. Copper sulphate and rotenone as fish poisons. Amer. Fish. Soc., Trans. (1939), **69**: 141–157.

SNEDECOR, G. W. 1940. Statistical methods. Collegiate Press, Ames, Iowa, 422 pp.

TRIPPENSEE, R. E. 1937. Fish population studies of some New Hampshire trout streams. New Hampshire Fish and Game Dept., Survey Rept., **2**: 119–124.

SHARP-TAILED GROUSE IN THE SAND DUNE COUNTRY OF NORTH-CENTRAL NORTH DAKOTA

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This study was a cooperative project between the Fish and Wildlife Service and the Lake States Forest Experiment Station. Many of the field data were collected by Donald Manning, with headquarters at the northern branch of the Experiment Station at Denbigh, North Dakota. The field work extended from August 1937 to the spring of 1939, but most of the material reported pertains to the autumn and winter.

Investigations were confined to McHenry County, but the findings apply to the entire sand dune area (Pl. 1, *A*, *B*) of north-central North Dakota, mostly in McHenry, Pierce, and Bottineau counties, of about 200,000 acres and largely tax delinquent. About 10 per cent of the area is occupied by the dunes, some actively shifting and others fairly stabilized by vegetation (Pl. 2, *A*, *B*).

Most of the area is part of the bed of glacial Lake Souris, now restricted to the Souris River and marshlands. About 90 per cent of the land is level to slightly rolling and has more or less grass, which is cut annually for hay in the flatter meadows. Lower areas are marshy and mostly within the Lower Souris Na-

tional Wildlife Refuge. Practically all privately owned land here is used for grazing and wild hay production, a very small acreage being in cultivation.

The permanent water table is 6 to 12 feet below the surface of the flat land; little fluctuation is noticeable, even in droughts. The climate is sub-humid, with long cold winters and relatively short cool summers, the temperatures varying from +105 to −50°F.

Barbed-wire fences are common to control grazing and are outstanding ecological barriers, particularly among the dunes, where a fence often divides shifting sands and an area stabilized by vegetation. The experiment station land has been fenced against grazing since 1931 and the benefits are very apparent (Pl. 1, *A*, *C*, *D*). Poison ivy is a dominant plant on overgrazed tracts, but is scarce on those free from excessive use by livestock.

The local flora comprises many species. Those more important for grazing and wildlife utilization include, among the dominants: Porcupine grass, blue grama, little bluestem, big bluestem, cord grass, green pigeon grass, slender wheat-grass, wild oats, lambs-quarters, lead plant, little sage, rose, wolfberry, sunflower, and marsh elder. Most of the trees and shrubs grow on the sand dunes; these include box elder, hackberry, bur oak, Juneberry, red haw, chokecherry, and horizontal juniper. There are scattered clumps of aspen and willow on the lowlands. Along the Lower Souris River bottoms there is an abundance of woody plants, common trees being the cottonwood, aspen, box elder, green ash, and bur oak.

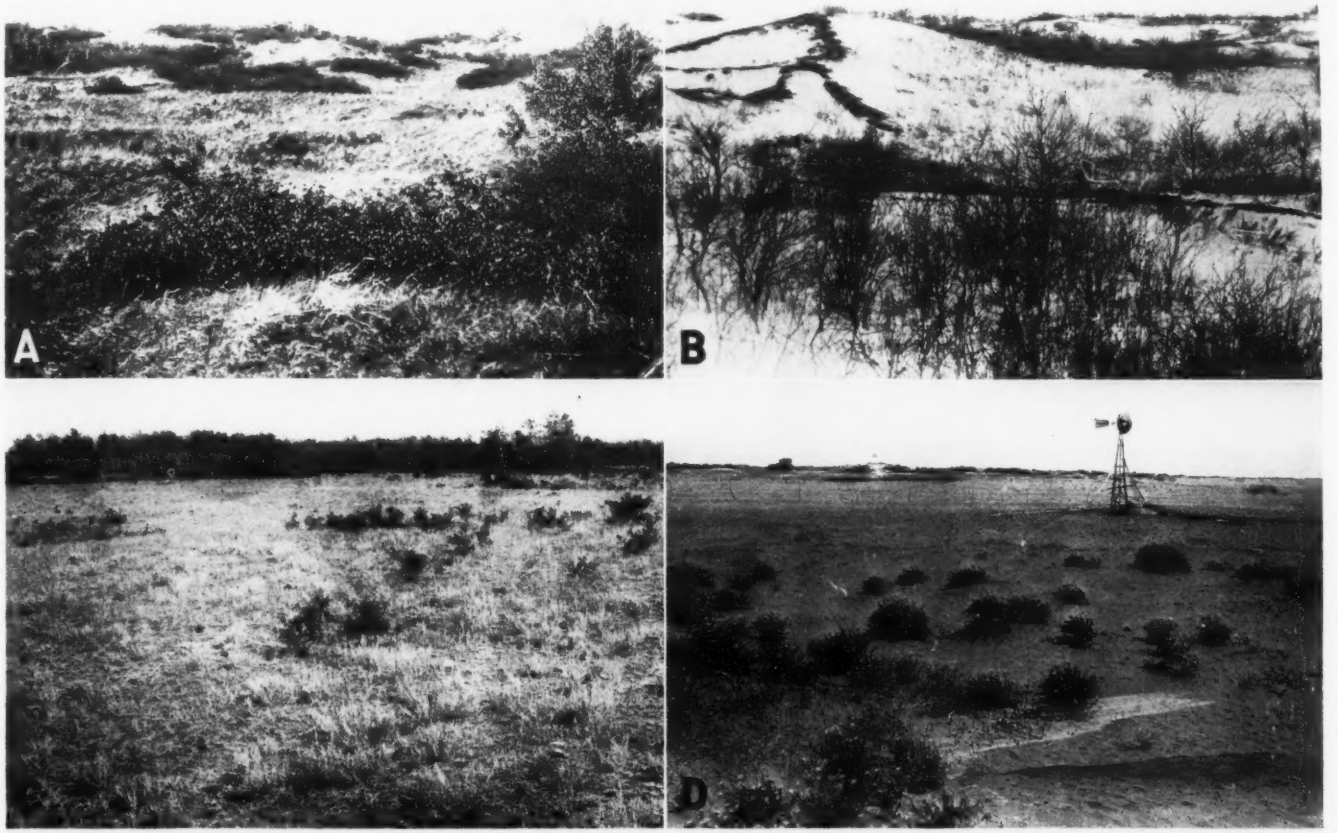
GAME SPECIES

The sand dune area is often referred to as "Little Siberia." To one unacquainted with wildlife requirements it appears to be a very unsuitable habitat, but is rich in wildlife. Waterfowl find a haven on the marshes and waters of the Lower Souris National Wildlife Refuge and have greatly increased under the improvement program of the U. S. Fish and Wildlife Service, but must leave when ice covers the water.

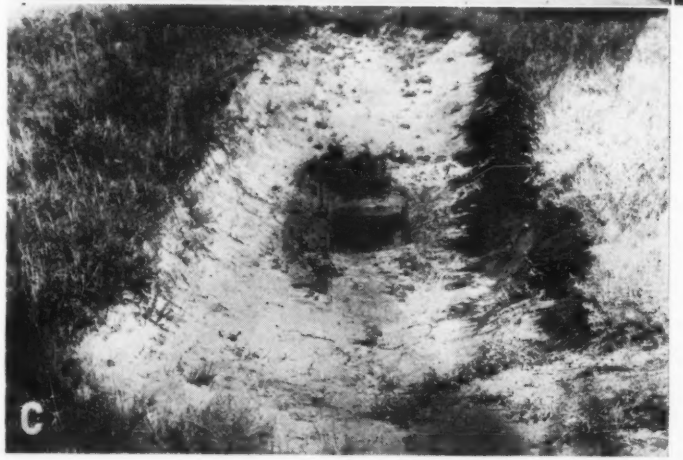
Species not dependent on open water are present on the uplands throughout the year. Ring-necked pheasants and Hungarian partridges have both been successfully introduced, but depend on cultivated grains so they probably will never become abundant. Sharp-tailed and pinnated grouse are the only native upland game birds now present, the former being far the more numerous. Their populations probably are the best anywhere in the northern plains region and have been maintained despite open seasons almost every year. Ruffed grouse live in the Turtle Mountains to the north and east but not in the dune country; in time proper cover for them may develop in the sand hills. White-tailed deer occur in moderate numbers chiefly in the Souris River bottoms where trees and shrubs afford better protection than the sparse vegetation of the dunes; deer are often seen, however, in the open meadows and around the sand dunes.

Throughout the area white-tailed jack rabbits and cottontails are sufficiently numerous to damage severely the shelterbelt plantations and field and garden crops.

J. H. Stoeckeler of the U. S. Forest Service took a wildlife census on 6,560 acres of dune country in November 1936, and made population estimates



Sand dunes near Denbigh, North Dakota. *A*. Summer. Brush is mostly chokecherry, with aspen in background. Area protected from grazing by livestock. *B*. Winter. Brush mostly chokecherry; exposed dunes are windswept. *C*. Flat between dunes. Shrubs are mostly wild rose and trees are aspen. Excellent forage areas for sharp-tailed and pinnated grouse. *D*. Overgrazed area near watering places; even the dunes beyond are bare. This condition is disastrous for wildlife, livestock, and farmers. (Photos by U. S. Forest Service.)



A. Shifting sand dune, Lower Souris National Wildlife Refuge, Upham, N. D.; all grazing should be eliminated. *B*. Old "blow-out" in sand dunes partly stabilized by vegetation since grazing was eliminated. *C*. Water hole made with scraper; water level about 8 feet below surface. (Photos by U. S. Forest Service.)

for the Souris Purchase Unit (483,000 acres) as follows:

Sharp-tailed and pinnated grouse	4,000
Hungarian partridge	1,200
Ring-necked pheasant	500
White-tailed deer	100 to 150
White-tailed jack rabbit	21,000
Cottontail rabbit	1,000

SHARP-TAILED GROUSE

The dominant upland game bird in the sand dunes is the sharp-tailed grouse (*Pedioecetes phasianellus*) as shown by censuses and trapping; hence the birds are easy to study and most of the life history data reported here pertains to this species.

Trapping and Banding. These grouse are relatively easy to trap when the ground is blanketed with snow. Toward spring, when bare spots appear, even though the temperature is low and most of the landscape is still snow-covered, trapping is less successful. During the winter of 1937–38 only 21 were trapped, the first on December 30 and the last on March 28, as the weather was moderate and bare spots were common during much of the season. The following winter sharptails first entered the traps on October 8 and by February 25, 79 previously unmarked birds had been caught and banded. They soon learned that the traps afforded a ready source of food and many were recaught. Of the 100 banded, 32 reentered the traps once, 7 twice, 2 thrice, 3 four times, 3 five times, 1 six times, 1 eight times, and 1 nine times. Fourteen of the 100 birds banded are known to be dead.

Their daily and seasonal movements are not great. Band and trap returns indicated the greatest movement as 58 miles, by one bird. It was banded at Denbigh, January 9, 1938 and shot at Antler, October 12, 1940. Others traveled 31, 7, 6, 4, and 2 miles, respectively. Two birds moved 1 mile, 1 a half mile, and 21 one-fourth mile each; the latter group traveled between two trapping stations. The one that travelled 31 miles was caught at Denbigh on December 19, 1938, released 11 miles to the east, and retaken 20 miles northwest of Denbigh on October 11, 1939. Its movement may have been influenced by transfer to a strange environment. No returns have been received from other birds released at points at some distances from their places of capture. The longest interval between banding and return was 2 years, 9 months.

The large number of retrapped individuals and data on the sex of birds shot during the winter make it apparent that both sexes remain in the area throughout the year. Beliefs that the grouse migrate south, or that one sex migrates, are not supported by these findings.

Six traps of the tip-top type were used, with ears of corn impaled on nails around three sides of the top of the trap serving as bait. The traps were either covered with burlap or embedded in straw or snow. Areas around the traps were baited and after the grain there was consumed the traps were the only source of food. Established feeding stations are good locations for traps, but the regular food supply needs to be reduced so as to make the trap bait more attractive.

Parasites. The viscera of 34 sharp-tailed grouse were submitted to O. W. Olson and Arnold Erickson of the Parasitology Department of the University of Minnesota. One grouse har-

bored a tapeworm (*Railletina* sp.) and three had another cestode (*Rhabdometra millicollis*). The lice submitted were identified as *Goniodes* sp.; some birds were heavily infested with lice and others relatively free.

Mortality Factors. The common predators in the area that seemed likely to prey on grouse were golden eagles, accipitrine hawks, coyotes, skunks, weasels, and bull snakes. One grouse in a trap was killed by a weasel. No other predation was noted. Once a golden eagle soared around a group of dunes until five sharp-tailed grouse flew out, but the eagle made no attempt to attack the birds. Collisions with telephone wires, barbed wire fences, and speeding automobiles result in some mortality.

Food Habits. The food of this grouse is fairly well known for the autumn when considerable material is available from hunters, but the winter diet, usually the limiting factor in their existence, is poorly known. Twelve birds collected in winter under permit from the North Dakota State Game Department and three other specimens found dead during the winter were used for stomach analyses. The contents of 19 gizzards and 6 crops of autumn birds also were examined. The findings were supplemented by field observations. The foods from all of these are listed in Table 1.

Table 1.—FOOD OF SHARP-TAILED GROUSE IN MCHENRY COUNTY, NORTH DAKOTA. (Percentages)

Food item	Autumn				Winter				Occurrence Field Observations
	19 Gizzards		6 Crops		15 Gizzards		15 Crops		
	Vol.	Occur.	Vol.	Occur.	Vol.	Occur.	Vol.	Occur.	
Animal	9	47	36	100	1	27	2	27	—
Orthoptera	9	58	36	100	1	27	2	27	—
Other insects	tr.	5	—	—	tr.	7	tr.	9	—
Vegetable	91	100	64	100	99	100	98	100	—
Gravel	tr.	40	—	—	1	33	—	—	—
SEEDS:									
Ambrosia	tr.	5	—	—	—	—	—	—	—
Polygonum	1	32	1	100	tr.	7	—	—	—
Lithospernum	3	5	—	—	—	—	—	—	—
Setaria	tr.	5	—	—	—	—	—	—	—
Symphoricarpos	1	40	—	—	2	47	tr.	18	6
Rosa	55	95	60	100	80	100	15	91	14
Prunus	15	32	—	—	—	—	—	—	—
Crataegus	4	5	—	—	—	—	—	—	—
Rhus toxicodendron	2	16	—	—	—	—	—	—	—
Miscellaneous	tr.	11	tr.	17	1	13	tr.	9	tr.
Corn	2	11	tr.	20	3	7	—	—	—
Oats	1	5	—	—	tr.	7	—	—	—
Wheat	2	16	3	17	tr.	7	tr.	9	—
BUDS:									
Populus	tr.	23	tr.	33	3	67	14	82	8
Prunus	tr.	11	—	—	5	67	17	73	30
Salix	—	—	—	—	2	67	41	90	39
Quercus	tr.	5	—	—	—	—	—	—	—
Amelanchier	tr.	5	—	—	tr.	13	1	36	3
LEAVES	5	53	tr.	17	3	13	10	27	—

By October the birds had shifted to a diet largely of vegetable matter. Early frosts kill most of the local insects and those eaten in fall and winter are largely dead specimens. When occasional spots of bare ground are visible, the birds resort to them for feeding and dusting. Dried grasshoppers are common in such places and are the source of much of the winter insect food. Other insects taken during the winter were a chrysomelid beetle, a pentatomid bug, and a lepidopterous larva.

The seeds and fruits eaten represented 16 genera. In addition to those listed, sweet clover (*Melilotus*), vetch (*Vicia*), dandelion (*Taraxacum officinale*) and some unidentified seeds were taken. The most important food during both fall and winter was fruit of the wild rose. The hips can be found on the plants at all times of year and are particularly valuable during the winter, They are large and easily obtainable which adds to their value as a game food. Small grains are not important as food in this area primarily because of their scarcity.

Buds of plants of four genera were used during the winter and, with rose fruits, comprised most of the seasonal diet. Willow buds were the most important both by volume and frequency. The foliage eaten included the basal leaves of sage brush (*Artemisia*), rose, willow, currant, goldenrod (*Solidago*), and dandelion (*Taraxacum*). The sage leaves were consumed in the greatest quantity and most frequently.

Winter field observations on food habits were made by following the tracks of birds and recording the plants apparently sampled. One tally was made for each unit of space that a bird could forage over without moving, generally about one foot of trail. Each trail was followed for about 100 feet and then another was sought. Calculations from a total of 1,085 such records afforded the frequencies of feeding noted in Table 1. Those for willow buds exceeded all others and in every instance there was heavy disbudding. For the other three species tabulated, only light budding was recorded. The trace of miscellaneous seeds eaten represents five observations of feeding on the seeds of sage brush (*Artemisia*).

The short list of foods utilized by these birds, especially in winter, verifies the statement by Swanson (Journ. Wildl. Mgt., 4, 432–436, 1940) that the dietary requirements of the sharp-tailed grouse are simple. This is an advantage in connection with management of the food supply.

Water Requirements. During the winter the birds apparently require moisture other than that supplied by buds. One bird was observed eating snow, about 30 bites being taken.

Feeding Mannerisms. When the birds are eating buds on low vegetation, they wander aimlessly among willows, aspens, chokecherries, etc., sometimes recrossing their own trails. They do not completely disbud any one group of shrubs, but feed on both sides of the trail as they progress. For no apparent reason and certainly not because of lack of food, they will leave one clump and wander across barren snow, sometimes a hundred yards, to others and resume feeding.

To observe some of their feeding habits, a station was established about 300 yards from the headquarters house, to which point a group of birds came

every day. It consisted of a flat board bearing several ears of corn impaled on nails which was moved toward the house a few yards each day until it was within 30 feet of the front window.

The birds that fed here varied from 1 to 15, averaging 4 in 1938 and 9 in 1939. The increased use in the second year was undoubtedly because older birds returned with their young. The same group of birds frequented the station, most of them being observed to bear leg bands.

Their time of arrival each morning varied, being influenced by the hour of sunrise and the degree of light. On stormy days they were usually later, but not always. After several days of stormy weather they came earlier, suggesting they had not fed regularly elsewhere during the storm. The relation between their time of arrival and sunrise is shown in Figure 1.

The birds did not fly directly to the station, but alighted 50 to 100 feet away and approached on foot in a cautious and hesitant manner, with many stops and surveys for danger. Then they greedily consumed the corn by pecking it from the top of the cob downward. An individual bird would seldom feed wholly at one ear, but would go from one to another as if there might be something better on the next one. When several birds were present, one was aggressive and tried to keep the others from feeding, resulting in much commotion. After feeding until satisfied, they sometimes walked a few feet away from the station and squatted in the snow, occasionally remaining for an hour, but sooner or later activity in and around the house caused them to flush. Infrequently they would return around noon for a second feeding, and once in the evening.

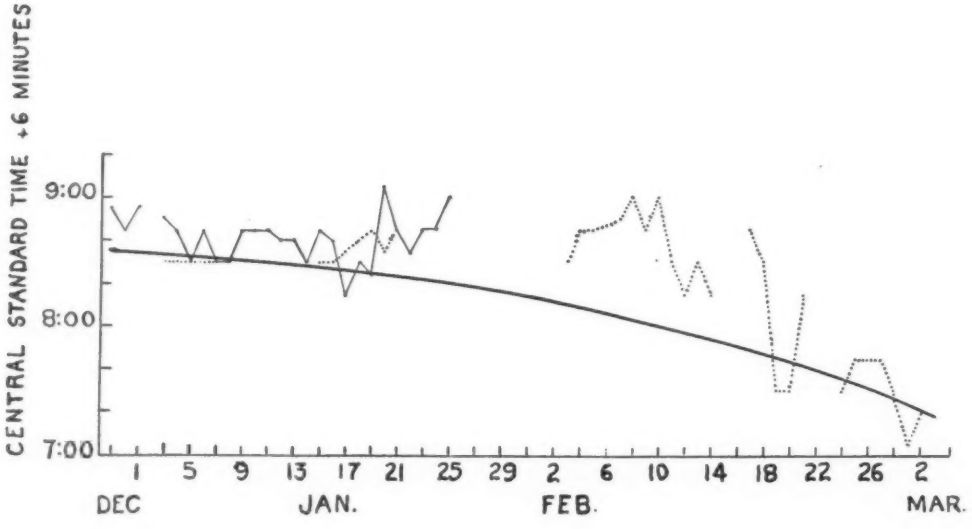


Fig. 1. Morning arrival of sharp-tailed grouse at feeding station, Denbigh, North Dakota, in relation to sunrise; · · · , 1937–38; ——, 1938–39; continuous curve, sunrise Central Standard Time. Average deviation from sunrise, 18 minutes.

In general, more came to the station and they stayed longer during the midwinter. Toward spring, or when bare spots of ground appeared, the feeding periods became shorter and there were fewer birds. This decline in use of the feeding station coincided closely with decline in trapping success.

Weights. During the trapping, the birds caught were weighed whenever possible. These records and a few from birds collected for specimens, are summarized as follows:

		Weights in grams		
Season	*Weighings*	*Maximum*	*Minimum*	*Average*
Oct.–Dec.	82	1,020	632	894
Jan.–Mar.	67	1,031	734	862

Several weighings of some birds are included. The two lightest were undoubtedly late young of the year. It would be expected that the average weight would decrease during the severer part of the winter, but the reduction was less than anticipated, probably because the birds weighed were repeaters in the traps and benefiting by feeding on bait. Individual retrapping records revealed nothing definite as to physical condition; some fluctuated, others gained, and still others lost weight. The only way to obtain accurate data on seasonal variation would be to collect specimens where artificial feeding is not being practiced. The data show that feeding helps the birds through a difficult winter but is not necessary.

Breeding Data. A few records were obtained in 1938, as follows:

June 18, nest with 7 eggs in grass and wolfberry bushes.

June 20, hen with 7 chicks in cottonwood thicket.

June 22, hen and three chicks flushed.

June 23, hen on nest.

June 28, eggs all hatched and birds gone.

MANAGEMENT SUGGESTIONS

Grazing should be eliminated from all the dune areas by fencing to restrict livestock to the flat lands between the dunes. This will not reduce the stock carrying capacity of the general area as there is little feed on the dunes proper. When stock are excluded, the dunes gradually become stabilized and support a vegetative cover valuable to upland game birds (Pl. 2, *B*).

Annual harvesting of wild hay from the flats will not be detrimental to the game birds if done after the nesting season. Late in summer the mowed fields provide ideal feeding places for the birds, grasshoppers being particularly abundant.

Supplemental feeding of sharp-tailed and pinnated grouse is normally not required, but when necessary corn on the ear or buckwheat will both be eaten readily. Pheasants and Hungarian partridges might be encouraged and increased on the dunes by increased winter feeding as they are more dependent on grains than the native species.

The planting of shrubs and trees on and around the dunes will greatly benefit wildlife and will help to stabilize the dunes. Fast-growing trees and shrubs at the dune bases soon provide shade and cover for wildlife and also reduce the blowing of sand.

For a management program, knowledge of the important food and cover species is necessary. The following plants are valuable for upland game birds of the sand dune country.

Chokecherry (*Prunus virginiana*).—Growing from 4 to 12 feet high here, this is the dominant shrub of the dunes, usually on the eastern and southern slopes; the bigger the dune the thicker and larger the cherry bushes. It is im-

portant as summer cover for wildlife and serves as a windbreak and shelter in winter. The fruit ripens late in July, and until late fall is an important food item. The sprouted pits are reported to serve as food in spring. Grouse droppings collected August 9 were made up wholly of cherry pits and pulp. In any planting on the dunes, chokecherry should be used.

Dwarf rose (*Rosa pratincola*).—This grows from a few inches to 3 feet in height, depending on the soil type and plant competition. It is hardy and about the only important food plant that will thrive on over-grazed land. It is found everywhere except in extremely marshy places, and is one of the most valuable food and cover plants for upland wildlife. The plants produce good cover in summer and an abundance of fruits (rose hips), that persist on the plants throughout the year. The 1937 crop was very good; plants not over 6 inches high commonly bore several mature hips. Grouse droppings often are entirely of remains of these fruits. Artificial propagation is usually not necessary as the plant seems to establish itself wherever conditions are favorable. If absent from any sizable area, it would be excellent in a planting program.

Wolfberry (*Symphoricarpos occidentalis*).—This local "buckbrush," 1 to 3 feet high, grows most commonly on small rises in flat grass land where its dense mat of branches makes good cover for game birds over areas of 20 to 100 feet square. There were good crops of berries in 1937 and 1938, ripening in September and persisting on the plants all winter, that provided good food for upland game. The plant is worthy of consideration in any improvement program.

Juneberry (*Amelanchier alnifolia*).—This is most common on the dunes and is 2 to 10 feet in height. It is important as cover and the fruit is eaten by various birds. The 1937 berry crop was scant. The fruit ripens in July and persists on the bushes until after frost. The buds are an important winter food of sharp-tailed grouse.

Red Hawthorn (*Crataegus chrysocarpa.*)—This shrub, 4 to 10 feet high, is found chiefly on the dunes and forms good summer and winter cover. The fruits are eaten by many birds and mammals, ripening just before the frosts, and are usually sweeter and more palatable thereafter. It is an important food in early fall, probably eaten by all upland game birds. It can be propagated from either seeds or cuttings and more should be planted. In early August, 1937, all the bushes were loaded with unripe fruit.

Hackberry (*Celtis occidentalis*).—In the sandhill area this is a tree, 10 to 21 feet high, most common near the tops or in depressions of the dunes. The fruit is eaten by many birds but has not been listed in the dietary of any local game birds. It ripens about August and persists on the trees until the following summer, making an excellent winter food supply. In 1937, there was scarcely any fruit and the leaves were heavily infested with galls, which probably reduced their value as food for game. It can be propagated from seeds, and cuttings, or by layering. More of these trees would be desirable if only for their shade and windbreak utility.

Bur Oak (*Quercus macrocarpa*).—This oak grows along river bottoms and in the dunes, varying in form from a low shrub to large trees, and provides im-

portant cover and food for deer, squirrels, pheasants, and pinnated and sharp-tailed grouse.

Willows (*Salix* spp.).—These plants, particularly the dwarf willows (*S. humilis*), are extremely important for summer cover and winter food. Buds of the dwarf willow are one of the principal winter foods of the sharp-tailed grouse. Willows are easy to propagate from cuttings and should be included in any planting program where they are at present not well distributed. Moderate grazing and care to avoid cutting willow clumps with mowing machines are the only management practices needed to encourage them in the dune country.

Miscellaneous.—Trees, such as aspen, cottonwood, green ash, and others are important for cover and windbreaks and should be encouraged wherever they will grow.

The extent to which the grouse need a permanent water supply is unknown, but watering places add to the value of a habitat. Water holes can be scooped out in the flats by use of a scraper in a short time and the resultant water will be easily accessible to all forms of wildlife (Pl. 2, *C*).

SUMMARY

1. The sand dune areas of north-central North Dakota provide ideal habitats for upland game birds, particularly the sharp-tailed grouse. Pinnated grouse, Hungarian partridges, pheasants, white-tailed deer, jack rabbits, and cotton-tails also are present.

2. Sharp-tailed grouse are essentially resident throughout the year as shown by trapping and banding experiments. Their daily and seasonal movements, are usually for short distances.

3. The time when morning feeding begins accords closely with sunrise time.

4. The autumn food includes insects, weed seeds, small grains, and small quantities of buds. In winter the insect diet is drastically reduced and the seeds eaten are mostly those of wolfberry and wild rose. Buds make up the bulk of the winter food and are almost entirely those of *Salix*, *Populus*, *Prunus*, and *Amelanchier*.

5. Two cestode parasites and one species of louse were identified from the sharp-tailed grouse.

6. Management suggestions include: Elimination of grazing from the dunes; mowing of wild hay only after the nesting season; planting of good food and cover species on and around the dunes; and the provision of watering places where at present they are too widely separated.

FOOD HABITS OF THE BLUE GROUSE[1]

James Beer
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The food of the blue grouse (*Dendragapus obscurus* and *D. fuliginosus*) is known only in a general way. This paper reports on these grouse in Washington and northern Idaho and summarizes the published data on the subject over their entire ranges for a better understanding of their management.

Fig. 1. Map showing the areas studied (▨) and localities where stomachs were collected (black spots).

This study analyzes the contents of 128 stomachs (118 crops and 121 gizzards of *D. o. richardsoni* and 6 crops and 4 gizzards of *D. f. fuliginosus*). The birds were taken in Thurston, Cowlitz, Clark, Okanogan, Stevens, Asotin, and Garfield counties, Washington, Bonner and Latah counties, Idaho and Clackamas county, Oregon (Fig. 1). In addition analyses were made of 58 samples of droppings (totaling 322.2 cc.). The material was collected in 1939 to 1941, mostly in 1940 and in all months except March and May.

Most of the field observations were made in Okanogan, Cowlitz, and Clark counties, Washington, and in Latah County, Idaho. Notes by Dr. Leonard Wing, Wayne Tidyman, and Jacob Beer supplement observations by the author.

Methods

The food habits of birds are best determined by combining stomach examinations, analysis of droppings, and field observations. The principal reliance here is upon examination of stomach contents. The stomachs were weighed when first collected and then dried. The crop and gizzard contents then were placed in separate coin envelopes and saved for future examination. Later the materials were sorted, identified, and measured volumetrically, and the food percentages were calculated.

The droppings were obtained during the fall, winter, and spring when the grouse were feeding mainly on conifer needles. These are not completely digested hence their identification is easy.

[1] This study was a cooperative project by the State College of Washington and the Washington Department of Game. The Idaho Department of Fish and Game helped by allowing birds to be collected in that state. Appreciation is expressed to Norman Knott and Chester Ball, of the Washington Department of Game for the material they obtained and for the use of their seed collection, and to A. C. Martin for identifying some seeds not in that collection.

Analysis of droppings was an aid in determining when the grouse changed from the winter diet of needles to other foods, and from the summer diet to needles. Analysis of summer droppings did not give satisfactory results. Material was obtained from all available habitats of the blue grouse.

FOOD MATERIALS

PINACEAE. In many areas, firs (*Abies*) produce most of the food; five species are used by blue grouse. With *Pseudotsuga* they supply the main winter foods. *Abies* provides 60 per cent of the year-round food in western Washington. Needles, buds, and pollen cones are eaten, and seeds occasionally. The grouse start to eat needles in September, by October are feeding on them almost exclusively, and do so until April when they change to other plant foods.

One bird in Cowlitz County, Washinton, April 3, 1941 contained 1.9 cc. of needles and 7.8 cc. of pollen cones of *A. grandis*. Birds wintering on Silver Star Mountain fed almost exclusively on needles of *A. nobilis*, and those on East Moscow Mountain, Idaho, browsed mainly on *A. grandis*, though some were using needles of Douglas fir (*Pseudotsuga taxifolia*). In both places they sought *Abies* almost exclusively, although many *Pseudotsuga* were present.

Trees of the genus *Abies* are highly important to these grouse and play a definite part in limiting their distribution. Except for the balsam fir (*A. balsamea*), ranges of western representatives of the genus almost coincide with those of the blue grouse (Fig. 2).

The larch (*Larix*) is sought during July, August and September, or until its needles are shed. It supplies 5 per cent of the yearly food and its needles apparently are even more palatable than those of the firs. They are used mainly when few berries are available. In Montana the first conifer needles eaten in autumn are of western larch (*L. occidentalis*), according to Cooney (6).

Blue grouse eat buds, pollen cones, and seeds of seven or more pines (*Pinus*). In this study pines supplied 5 per cent of the yearly food. In July the birds had eaten pollen cones of *P. albicaulis* on Rock Mountain, Okanogan County, Washington. Seeds of *P. ponderosa* composed 7.17 per cent of the August food in eastern Washington and northern Idaho, being taken by both adults and young. A grouse collected on Foggy Dew Ridge, Okanogan County, Washington, October 7, 1940 had eaten needles of *P. albicaulis*. Grinnell, *et al.* (9), Belding (5), Munro (13), Neilson (14), and Cooney (6) all report the use of various pines in areas scattered from California to Canada.

It has been the author's experience that even where parts of pines are taken, this is usually near either *Abies* or *Pseudotsuga*, upon which the birds depend for most of their diet.

Probably the most important food plant of blue grouse is the Douglas fir (*Pseudotsuga taxifolia*). Needles, buds, tender twigs, and seeds are used as a staple in winter, and to some extent during the remainder of the year. Douglas fir, however, contributed but 2 per cent of the yearly food in western Washington, doubtless because most of the grouse material collected there was from areas dominated by *Abies*.

The grouse turn to their diet of need-

les during September although some are eaten in August when they start up to the winter range. Douglas fir needles made 31 per cent of the food during September in eastern Washington and northern Idaho. From the last of Octo-

Fig. 2. Distribution of the blue grouse (*Dendragapus*) in relation to the white firs (*Abies*) and the Douglas fir (*Pseudotsuga*). Range of blue grouse enclosed by heavy line; distribution of white firs, ///; distribution of Douglas fir, \\\.

ber until March or April the birds ate needles exclusively and needles were 43.2 per cent of the yearly food (Table 1).

The distribution of the Douglas fir and of the Genus *Dendragapus* agree except that the grouse extends a little farther north (Fig. 2). Most of the blue grouse population is in the Douglas fir area as was noted in the 1850's by Cooper (7).

During the autumn, the blue grouse move up from the open breeding range to thick stands of timber or even to timberline where they winter. They may remain for some time in one tree or a small group, but the evidence shows they usually move from tree to tree and seldom remain in one for more than three or four days at a time. During the winter they generally form loose concentrations well up on the higher mountains or on the tops of the high timbered ridges. The trees where they winter are usually thickly branched and afford an abundance of easily obtained needles; severe weather does not seem to bother them. Under such conifers droppings may accumulate until a bushel or more lie in one place, especially under isolated and dwarfed trees near timber line. Where there are many grouse the quantity of droppings reminds one of a chicken yard.

No remains of the hemlock (*Tsuga*) were found in the stomachs examined, but this tree is important to the blue grouse in some localities. Belding (5) and Swarth (20) report hemlock as being used as food in California and Alaska, respectively. Jacob Beer noted on April 4, 1941: "A 'hooter' has been feeding in a hemlock tree since March 4, and is still there at this date. It usually started feeding about 6:30 A.M. and again about 2:30 P.M."

The noble fir and Douglas fir may be preferred to hemlock but the latter is not neglected and may be the primary winter food tree in some areas, especially those adjacent to the coast.

Needles of spruce (*Picea*) are only a minor part of the food; no bird had made an entire meal of them. Simpson (18) writes that the grouse in captivity

do not eat spruce needles if those of fir, pine, or hemlock are present.

Cooney (6) found juniper berries (*Juniperus*) in some birds he examined and Saunders (17) says that grouse in Montana feed on juniper twigs in winter. The plant is probably of little importance as 17 birds examined by the author from areas with an abundant supply had eaten none of it.

GRAMINEAE. Grass blades and a few seeds are consumed in a limited degree, comprising but a trace in the diet. They are probably taken accidentally and play no important part in the diet.

CYPERACEAE. The only grouse that ate sedges (*Carex*) was collected at timberline in Okanogan County, Washington. Its crop was completely filled with the seed heads of a small alpine sedge. This plant seems to be taken mainly by males that do not come down to the breeding grounds in summer, and it makes up but a trace of the yearly food. A few seeds of *Scirpus* were found in one gizzard.

LILIACEAE. Plants of *Disporum*, *Smilacina*, *Streptopus*, and *Calochortus* furnish but little of the diet. The first two genera were represented quite regularly in the gizzards, their hard seeds substituting for grit. *Streptopus* leaves were found once and fruits of all but the last. Judd (10) says that in Montana and Utah the birds were seen to feed on leaves, buds, and flowers of the Mariposa lily (*Calochortus*). Liliaceous plants, however, seem not to be important in the diet in any region.

SALICACEAE. Leaves and buds of aspen (*Populus tremuloides*) are eaten mainly in early summer, and comprised about 5 per cent of the yearly food. The crop of one adult male collected June 20, 1940 near Conconully, Washington, contained 15.2 cc. of leaves and a little animal matter.

No willow (*Salix*) was found in the stomachs examined, but Jacob Beer saw a "hooter" make an entire meal of willow buds and young leaves on March

Table 1.—FOOD OF 62 ADULT *Dendragapus obscurus* (percentages by volume).

	June	July	Aug.	Sept.	Average for year
No. of stomachs	4	31	15	6	62
Pseudotsuga	0.7	0.7	0.1	0.1	43.2
Abies					10.0
Arctostaphylos				67.7	6.7
Cercocarpos					5.7
Larix		3.0	46.9	2.3	5.2
Pinus		1.1	7.8		5.2
Populus	50.3				5.0
Amelanchier		29.8	8.3		3.8
Vaccinium	24.8	1.4	3.0		2.9
Ribes		26.7	0.2		2.7
Balsamorhiza	12.6	12.3			2.5
Eriogonum	2.6	8.9	0.6		1.2
Arceuthobium			6.8		0.7
Taraxacum	1.0	2.3	2.7		0.5
Agoseris	3.0	2.1			0.5
Fragaria	2.0	2.5			0.5
Trifolium				3.5	0.3
Carex	3.0	0.2			0.3
Picea	2.6				0.3
Crataegus	0.2	1.9			0.2
Symphoricarpos			1.6		0.2
Erigeron		0.9			0.1
Polygonum			0.8		0.1
Gramineae		T	0.6		0.1
Rosa			0.4		T
Gilia		0.1			T
Pachistima		0.2			T
Arnica		0.1			T
Epilobium			0.1		T
Undetermined plant foods		0.3			T
Totals of plant foods	97.0	98.5	85.9	99.9	98.0
Hymenoptera	2.0	1.3	13.2	0.4	1.4
Coleoptera	0.3	0.3	0.3		0.1
Lepidoptera	0.3	0.2			0.2
Diptera				0.4	T
Homoptera	0.3	T			T
Neuroptera	0.3				T
Orthoptera		T			T
Totals of animal foods	2.0	1.3	13.6	0.4	2.0

20, 1941 in Cowlitz County, Washington and three others were flushed from among nearby willows. Flint (8) and Preble (16) reported considerable use of willow by the grouse in Colorado and the Athabaska-Mackenzie regions respectively. Willow may be much sought for in the spring, its new leaves perhaps being a welcome change from the diet of conifer needles. Willow leaves are eaten mainly before the berry season commences.

FAGACEAE. Acorns were among the foods taken in central California (Belding, 5); Judd (10) also mentions them in relation to the blue grouse.

LORANTHACEAE. *Arceuthobium laricis* was eaten when the grouse were feeding on needles of larch but made only a trace of the yearly food in eastern Washington and northern Idaho. The largest quantities were taken in August. In Yellowstone Park Skinner (19) says that in winter grouse feed on the mistletoe (*A. americanum*) that is often common in lodgepole pines. In both cases it apparently is taken only while the birds feed on the host plant.

POLYGONACEAE. Leaves and flowers of *Eriogonum* are eaten, averaging 1.2 per cent for the year. Small quantities were taken regularly during the summer and early fall. Seeds and flowers of various smartweeds were eaten occasionally during July, August, and September. Taylor and Shaw (21) and Belding (5) found the grouse eating parts of *Polygonum bistortoides* and *P. polymorphum* respectively. This plant is not taken in any quantity.

RANUNCULACEAE. Barlow (3) reports that the blue grouse sometimes eat flowers of the wild columbine (*Aquilegia*). Marsh marigold (*Caltha*) was eaten by grouse examined by Flint (7) from the mountains of southern Colorado.

BERBERIDACEAE. Van Dersal (22) states that *Berberis aquifolium* is eaten by the dusky blue grouse. This and closely related species are found over much of the grouse range but only once was noted as eaten, so that they probably are of no importance in the diet.

CRUCIFERAE. Seed pods of *Capsella Bursa-pastoris* were found in small quantities in some young grouse taken in Okanogan County, Washington during August.

SAXIFRAGACEAE. Seven species of *Ribes* have been listed among food plants of these grouse. Probably all species throughout the range of blue grouse are used. In eastern Washington and northern Idaho, currants made 2.7 per cent of the yearly food of adults and were taken by the young in larger quantities than any other plant food. The birds concentrate on them when the berries are ripe. The young climb in the bushes or jump to obtain the berries and adults take berries that can be reached from the ground. The grouse feed on them until all are consumed or dried up. Fruits of *Ribes* were present in quantities in the birds examined but should not be considered an indispensable food except perhaps on waterless ranges.

The large quantities in the stomachs probably reflect their abundance in the areas where the young grouse were collected. The local distribution of the grouse is probably affected only to the extent that the birds will move short distances to feed on wild currants.

Over much of the territory of the Richardson and dusky blue grouse currant plants are being removed in an attempt to eradicate the white-pine blister rust. Areas in northern Idaho where this program has been carried on show no detrimental effects so far as supporting the grouse is concerned. No young from that region were examined so it is impossible to say what food replaced the *Ribes* fruits.

Belding (5) writes that old as well as young birds appear to be very fond of the miterwort (*Mitella breweri*).

ROSACEAE. Service berries (*Amelanchier* spp.) formed 3.8 per cent of the total diet of the adults examined and were used extensively by the young. They are eaten mainly during July and August, being a favorite summer food obtainable practically throughout the range of the blue grouse. Both young and old climb around in the bushes and feed on the berries like ruffed grouse. By the time the wild currants are gone the service berries are ripe and the diet changes accordingly. *Amelanchier* bushes furnish both food and cover during the summer.

Two gizzards from the Blue Mountains in southeastern Washington contained a quantity of leaves of mountain mahogany (*Cercocarpus*). The extent to which it is eaten and its relative importance are not known.

The berries of hawthorns (*Crataegus*) made but a trace in the yearly food, but the areas where the birds were collected had but little. Two taken where berries were available had fed on them more than on any other food. Where hawthorns are abundant they probably form a major part of the diet during the period when available. Munro (13) states that when the supply of fallen pine seeds is exhausted the grouse eat red and black haws.

Wild strawberries (*Fragaria*) made less than one per cent of the diet, being like most fruits taken in direct proportion to availability. Bailey (1) states that on Pecos Baldy the birds lived on such food as strawberries. The wild strawberries are among the earlier fruits available and are probably sought as much as any other fruit.

One bird killed in October in the Blue Mountains, Washington had eaten leaves of ninebark exclusively.

Pits of chokecherry were found in the gizzards, but none in the crops, being used as a substitute for grit. Fruits of *Prunus* probably are of minor importance as several birds were taken from areas where choke-cherries were available.

Leaves of the mountain ash (*Pyrus*) were eaten by grouse collected from the Mount Rainier area (21) and Belding (5) reports these berries in some of the stomachs examined by him. Mountain ash is usually found at fairly high elevations where huckleberries are common; the latter seem to be preferred.

Rose hips are eaten by these grouse, though seldom in any quantity. One bird taken August 18, 1940, in Okanogan County, Washington had twelve rose hips in its crop. This is the only instance to which rose was the sole food. Rose seeds were present in about 15 per cent of the samples of droppings and gizzard contents.

Preference is given to fruits of *Rubus* over nearly any other food. They formed 17.5 per cent of the yearly diet

in western Washington, but were present only as traces in eastern Washington and northern Idaho. The difference is due to availability. In the burns and logged-off areas of western Oregon and Washington, fruits of *Rubus macropetalus* comprises a high percentage of the summer food, and takes the place of both the *Ribes* and *Amelanchier* which are much used in eastern Washington and northern Idaho. The sooty blue grouse follows the ripening of the wild blackberries until the last of the berries at high altitudes are gone. Salmon berries, raspberries and thimble berries are eaten whenever available.

LEGUMINOSAE. Leaves of clover (*Trifolium*) comprised only a trace of the food. An occasional seed of lupine was found in a few crops and gizzards.

CELASTRACEAE. Seed pods of *Pachistima myrsinites* made but a trace of the food, seeds being found in two crops and in several gizzards.

ELAEAGNACEAE. Seeds of *Shepherdia canadensis* were found in the gizzards of two birds collected August 14, 1940 and one taken in July in Okanogan County, Washington. Materials of this genus have been reported as blue grouse food seven times in the literature.

ONAGRACEAE. Seed pods of *Epilobium* were taken during the last week of June in small quantities, one adult and several young grouse having eaten them.

UMBELLIFERAE. Belding (5) reported *Glycosma* from grouse collected in central California.

CORNACEAE. Van Dersal (22) lists *Cornus* as being eaten by the Richardson grouse.

ERICACEAE. *Arctostaphylos uva-ursa* berries were taken to the extent of 6.8 and 13 per cent of the yearly food in eastern Washington and northern Idaho and in western Washington, respectively. Fruits of this genus and especially the bearberry are one of the most universally used blue grouse foods. The berries are eaten at all stages of development, although ripe ones are preferred. Two crops collected during the last week of August 1940 about 15 miles southwest of Government Camp, Oregon contained only bearberries and huckleberries. The fruits are useful as food and their seeds serve as grinding material. In several of the gizzards examined these seeds were the only such substance present.

Simpson (18) reports that blue grouse kept in captivity at Nehalem, Oregon ate some cranberries.

Salal berries (*Gaultheria shallon*) are eaten in large quantities by grouse in the coastal areas of Washington, British Columbia, and Oregon. None of the birds examined by the author during this study had eaten any parts of this plant. This was due to the quantity of blackberries and huckleberries in the areas from which the specimens were taken.

In nearly all of the mountainous areas of the west there are one or more species of huckleberries (*Vaccinium*). Their fruits, leaves, and blossoms are eaten freely by the blue grouse at all stages of development. These plants contributed one and 3 per cent of the yearly food of the birds examined from western Washington, and from eastern Washington and northern Idaho, respectively. None of the birds was collected from the huckleberry ridges during the height of the berry season, so that these figures are probably much

too low to represent the average diet. The small bushes of most of the species of the genus make the berries readily available to the grouse. A crop from Bonner County, Idaho, August 10, 1940, examined by Robert Braunwart contained only the berries and leaves of huckleberries.

Various parts of huckleberry bushes are eaten throughout the summer and fall. The blue grouse do their last ground feeding on the high ridges where the huckleberries are the thickest before retiring to the conifers for the winter.

POLEMONIACEAE. A few seed pods of *Gilia gracillis* were found in three birds collected in Okanogan County, Washington.

SCROPHULARIACEAE. Bailey (2) reports that the flowers of paint bush are eaten by the blue grouse. Merriam (11) writes of a grouse taken on Mount Shasta that had fed on the seed capsules of *Pentstemon gracilentus*.

CAPRIFOLIACEAE. Belding (5) reports the mountain twinberry (*Lonicera*) as being used as food by the blue grouse in central California. Judd (10) also reports plants of this genus being eaten. Berries of various species of elderberry (*Sambucus*) are eaten at times by the blue grouse. Those of *S. melanocarpa* were found in the crop of one bird taken near Winthrop, Washington, August 11, 1940. Elderberries are not readily available to birds the size of a blue grouse and it is doubtful whether grouse normally eat them to any extent.

The berries of *Symphoricarpos* are eaten over much of the area occupied by the blue grouse, but they rank rather low on the palatability list of the grouse and are seldom taken in quantity even when the easiest food to obtain. Birds collected in areas containing large quantities of ripe snowberries had eaten but few of them, and formed less than one per cent of the yearly food of the grouse examined. It is probable that only in the absence of other fruits would many snowberries be eaten.

COMPOSITAE. The seeds of *Balsamorhiza* were taken in large quantities when ripe in June and July. In eastern Washington and northern Idaho they comprised 2.5 per cent of the yearly food of the adults, and the young eat them in even larger quantities. Small quantities of *Agoseris*, *Arnica*, *Erigeron*, and *Taraxacum* were found occasionally in the stomachs examined. Belding (5) and Simpson (18) report that *Wyethia mollis* and *Hypocheris radicata* are eaten by these grouse.

POLYPODIACEAE. A bit of bracken (*Pteridium aquifolium*) was found in the crop of one bird collected in Clark County, Washington, September 16, 1940.

ANIMAL MATERIALS

Animal food made only 1.7 per cent of the adult diet, but is very important to the young grouse. It is probably for this reason that the blue grouse usually nest in the open where there is an abundant supply of insects. During the first few days of life they feed almost exclusively on animal material (Fig. 4). When about ten days old the chicks start to eat plant foods. The insects most commonly taken belong to the Hymenoptera (Formicidae), Coleoptera, and Orthoptera. The stomachs examined yielded insects belonging to eight orders and occasional spiders, millipedes, and centipedes. Most of

the insects eaten were fairly large. The determining factor as to which was eaten most extensively was its abundance. Judd (10) records a snail (*Polygyra*) in the stomach of one bird.

used. Complete substitution of hard seeds for grit is rather common.

There is a fairly rapid replacement of grinding material when an abundant supply is available. The droppings often

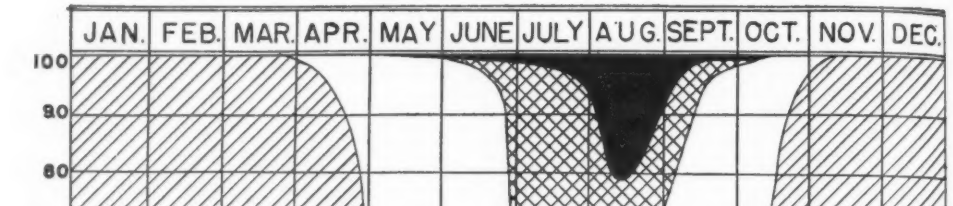

Fig. 3. Yearly food of 68 adult blue grouse.

GRIT

The grit in gizzards varied from none to 16 cc., and averaged about 6 to 8 cc. It was mostly uniform in size, about 4.7 mm. in diameter, but the extremes varied from sand grains to pieces of jagged rock 18 mm. long. Quartz was used wherever available.

Hard seeds are sometimes substituted for grit to grind the food (Beer and Tidyman, 4), those of *Arctostaphylos uva-ursa, Prunus, Rosa, Crataegus,* and even *Symphoricarpos* being

contain quantities of grit passed on from the gizzard. The average crop contained about 0.02 cc. of grit, and the most in any crop was 0.8 cc.

WATER REQUIREMENTS

Blue grouse are seldom found far from a source of water. The supply may be succulent vegetation or berries but is usually a spring or other body of water. During the summer, their tracks are almost always to be found around springs. On several occasions the author

has seen the birds drinking at these cold mountain watering places. One bird killed a quarter of a mile from the nearest known drinking place had considerable water in its crop. Free water is not necessary, however, if moisture is obtainable in succulent vegetation or fruits.

FOOD OF ADULTS

The adults are mainly vegetarian, eating 98 per cent of plant materials. Conifer needles comprised 63.8 per cent, berries 17.0, miscellaneous plant materials 17.2, and animal matter 1.7 per cent in the specimens examined. The proportions of these types of food throughout the year are shown in Figure 3. Some conifer needles are eaten at all seasons but they are most important during the six winter months. From about the first of November until the middle of April little else is eaten, species of *Abies* and *Pseudotsuga* being the principal sources. About the first of June the grouse commence to eat berries. In eastern Washington the first taken are usually those of *Ribes*, and in western Washington those of *Rubus*. In eastern Washington and northern Idaho the usual order of fruit-feeding is *Ribes* or *Fragaria* followed by *Amelanchier* and *Arctostaphylos* and ending with *Vaccinium*. In western Washington the progression of fruits eaten is *Rubus*, *Amelanchier*, *Gaultheria*, *Vaccinium*, and *Arctostaphylos*. The quantity of berries taken depends upon their availability. Blue grouse tend to follow the ripening of the berries in the fall migration to the higher levels where they spend the winter.

Animal food is of minor consequence so far as the mature birds are concerned, although in August it forms about 15 per cent of their food. Only the larger insects such as carpenter ants, beetles, and grasshoppers which are abroad in large numbers are eaten to any extent. Insects have been found in stomachs collected from June to October, and probably are taken during May but no records are available.

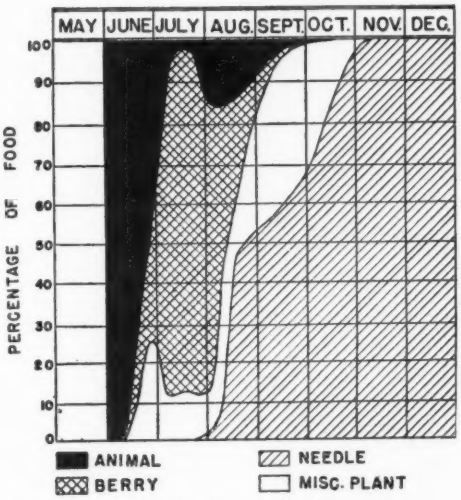

Fig. 4. Food of 60 young blue grouse.

The miscellaneous plant foods taken are so varied that it is impossible to say which are of real importance.

FOOD OF THE YOUNG

The youngest bird taken was nearly two weeks old. Moffitt (12) found 9 black beetles 5 mm. long, in the stomach of a bird about two days old. Probably no plant food is taken for the first few days. The average hatching date for eastern Washington is about June 1. The first group of young birds examined represented the third week in June; animal material then comprised 71.2 per cent of the diet, berries 23.5 per cent and seeds 5.3 per cent.

Availability of a good supply of insects during the first month of the chick's life is important. The quantity of insects taken decreases and that of berries

Table 2.—FOOD IN CROPS OF 60 YOUNG *Dendragapus obscurus* (percentages by volume).

	June	July	Aug.	Averages
No. of stomachs	6	25	31	60
Ribes	24.7	23.3	0.8	17.6
Amelanchier		30.9	1.1	14.0
Vaccinium		25.0	7.3	13.5
Arctostaphylos			25.9	8.6
Balsamorhiza	15.6	2.6	1.6	5.2
Taraxacum		0.9	8.3	2.2
Rosa			6.4	2.1
Symphoricarpos		1.2	3.5	1.7
Pseudotsuga		0.2	2.9	1.0
Carex			1.8	0.6
Agoseris			1.8	0.6
Eriogonum		0.8	0.6	0.6
Sambucus			1.4	0.5
Trifolium			0.9	0.3
Polygonum			0.4	0.1
Pinus			0.4	0.1
Capsella			0.3	0.1
Pachistima		0.2		0.1
Epilobium		3.2	0.3	1.5
Lupinus		T	0.1	0.1
Lithospermum		T		T
Larix			22.9	7.6
Gramineae		T	0.2	0.1
Disporum			T	T
Totals of plant foods	40.2	88.5	86.0	78.3
Orthoptera	12.9	9.5	3.1	8.2
Coleoptera	20.5	1.3	4.1	6.5
Hymenoptera	19.5	0.6	3.8	5.9
Diptera		T	1.9	0.7
Homoptera	0.4	T	0.1	0.1
Araneida		T	T	T
Lepidoptera		T	T	T
Chilopoda		T		T
Totals of animal foods	53.3	11.7	17.2	21.7

increases, until about the middle of July, when insects form only about 2 per cent of the food, the young then being about six weeks old. Their subsequent feeding is like that of the adults.

The young are fond of wild currants (*R. reniforme*) which are abundant on the east slope of the Cascades. They climb around in the bushes or jump from the ground for the berries. Later they band together, and the author has seen twenty or more in a clump of *Amelanchier* at one time. Besides these berries and the insects, they eat quantities of seeds and green materials. In eastern Washington they relish the seeds of the abundant *Balsamorhiza*.

TIME OF FEEDING

The records here cited are for birds collected between 6 a.m. and 8 p.m. from April to October. The grouse reach the peak of their morning feeding by 7 a.m. and by 9 a.m. quit and rest for an hour or so. Between 10 and 11 a.m. they again start feeding and continue until shortly after noon. After this minor feeding period they stop for about an hour. Then from 2 p.m. until 5 p.m. they pick around some but only enough to keep a little food in their crops. After this period of casual feeding they carry on the most intensive foraging of the day. By 7:30 p.m. the average crop contents of an adult weighs about 45 grams, about the maximum capacity. Field observations agree with these findings.

The birds go to water, when available, during the first half of the morning. It is not uncommon to see an old hen leading her brood of quarter- or half-grown young to a nearby spring or stream between 8 a.m. and 10 a.m.

The weight of the gizzard contents varies directly with that of the crop, but the fluctuations in the gizzard are not great and never so marked as with the crop contents. There is, apparently, a movement of food through the gizzard at all times. The effect of season on feed-

ing is mainly in the spring, when the males are "hooting" and the females nesting. The males feed and "hoot" intermittently during the day. Often an old male may be noted to grab a few needles or leaves, "hoot," and then snatch another mouthful of food, especially during the height of the breeding season. The time of day that the hens leave their nests is unknown.

The growing young feed more continuously than do the adults, but grouse of all ages do their heaviest feeding during the last three hours of daylight.

ECOLOGY AND LIMITING FACTORS

The distribution of birds of the genus *Dendragapus* appears to be determined by that of their food plants, coinciding for the most part with the range of the firs *Abies* (except for the balsam fir) and *Pseudotsuga*. Blue grouse are found mainly in the Douglas fir belt. Plants of these two genera provide about half of the yearly food of the blue grouse, their needles being fed upon almost exclusively during the winter. The birds also eat the needles of the white-barked pine, hemlock, and spruce, but winter in such trees only locally.

During the last of March and in April the blue grouse leave their winter homes in the firs on the high ridges and migrate to lower country where the snow has melted and there are openings in the forest suitable for rearing the young. A few non-breeding males remain on the high ridges throughout the summer.

The grouse remain in the breeding territory until the middle of July when they start following the ripening of the berry crop back up the mountain ridges where they spend the winter. When there is a failure of the berry crop, the birds move up the mountains more rapidly.

During the summer the birds may wander several miles from the nearest conifers but when autumn comes they go to the fir timber to spend the winter.

SUMMARY

1. Stomachs of 128 blue grouse from seven counties in Washington, two in Idaho, and one in Oregon were examined. Also 58 samples of droppings from three counties in Washington and two in northern Idaho were examined in the laboratory and many others in the field. All were analyzed volumetrically.

2. Parts of plants of 69 genera are known to be eaten by the blue grouse and representatives of 45 of these were found in the stomachs examined. Plant foods of 16 genera and 27 species are here reported for the first time.

3. The yearly food comprised 98.3 per cent of plant foods and 1.7 per cent of animal matter. Of this 63.8 per cent is needles, 17.0 per cent berries, and 17.2 per cent miscellaneous plant materials.

4. Little animal matter is taken by adults, but the food of the young is entirely of insects at first; by the middle of August it becomes the same as that of the adults.

5. The birds have three feeding periods. The first early in the morning, the second just before noon, and the third and heaviest during the last three hours of daylight.

6. Free drinking water is not necessary for the blue grouse.

7. The distribution of the genus *Dendragapus* appears to be limited by that of the plant genera *Abies* and *Pseudotsuga*.

LITERATURE CITED

1. BAILEY, F. M. 1904. Additional notes on the birds of the upper Pecos. Auk, **21**: 351.
2. 1904. Handbook of the birds of the western United States. Boston, Houghton, Mifflin and Co., p. 351.
3. BARLOW, CHESTER. 1901. A list of the land birds of the Placerville-Lake Tahoe stage road, Central Sierra Nevada. Condor, **3**: 160.
4. BEER, JAMES and WAYNE TIDYMAN. 1941. The substitution of hard seeds for grit. Journ. Wildl. Mgt., **6**: 70–82.
5. BELDING, LYMAN. 1892. Food of the grouse and mountain quail of central California. Zoe, **3**: 232–233.
6. COONEY, R. F. 1938. Our upland game birds. U. S. Forest Service, Northern Rocky Mountain Region, Field notes on wildlife, **1**(1): 4–5.
7. COOPER, J. G. 1860. Pacific Railroad Reports.—Zoological report. Washington, D. C., **12**(2): 220.
8. FLINT, H. R. 1928. Some Rocky Mountain grouse. Am. Forests, **34**: 601–602.
9. GRINNELL, J., S. DIXON and J. M. LINSDALE. 1930. Vertebrate natural history of a section of northern California through the Lassen Peak region. Univ. Calif. Publ. Zool., **35**: 200.
10. JUDD, S. D. 1905. The grouse and wild turkeys of the United States and their economic value. U. S. Biol. Surv. Bul., **24**: 41–44.
11. MERRIAM, C. HART. 1899. Results of a biological survey of Mount Shasta, California. U. S. Biol. Surv., N. Amer. Fauna, **16**: 110.
12. MOFFITT, JAMES. 1938. The downy young of *Dendragapus*. Auk, **55**: 589–595.
13. MUNRO, J. A. 1919. Notes on some birds of the Okanagan Valley, British Columbia. Auk, **36**: 65–67.
14. NEILSON, J. A. 1926. Bird notes from Wheatland, Wyoming. Condor, **28**: 99–100.
15. PEARSON, G. T. 1923. Birds of America. New York, University Society Inc., Vol. **2**: 13.
16. PREBLE, E. A. 1908. A biological investigation of the Athabaska-Mackenzie region. U. S. Biol. Surv. N. Amer. Fauna, **27**: 337.
17. SAUNDERS, A. A. 1914. Birds of Teton and northern Lewis and Clark Counties, Montana. Condor, **16**: 130–131.
18. SIMPSON, GENE. 1935. Breeding blue grouse in captivity. Am. Game Conf., Trans., **21**: 218–219.
19. SKINNER, M. P. 1928. Yellowstone's winter birds. Condor, **30**: 240.
20. SWARTH, H. S. 1911. Birds and mammals of the 1909 Alexander-Alaska expedition. Univ. Calif. Publ. Zool., **7**: 56–58.
21. TAYLOR, W. P., and W. T. SHAW. 1927. Mammals and birds of Mount Rainier National Park. U. S. Dept. of Interior, p. 138.
22. VAN DERSAL, W. R. 1939. Native woody plants of the United States, their erosion control and wildlife values. U. S. Dept. of Agric., Misc. Publ., **303**: 1–362.

FUR YIELD AND AUTUMN FOODS OF THE RACCOON IN ILLINOIS RIVER BOTTOM LANDS[1]

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Illinois is properly considered a prairie state, but has several large river bottom areas. On the west, south, and southeast it is bounded respectively by the Mississippi, Ohio, and Wabash rivers for over 1,000 miles. In addition, the Illinois River Valley, long a famous region for fish, waterfowl, and fur animals, extends nearly 300 miles northeasterly through the state. The Rock River in the north, the Sangamon in the center, and the Embarras and Kaskaskia rivers in the south, add materially to the bottomlands. Bounding and interior streams have flood plains in Illinois aggregating over 4,500,000 acres, more than half of which is forested (Case and Myers, 1934). In some contiguous and southern states the flood plain type may reach even greater proportions. This habitat has always been important for wildlife, and of late years is of increased significance with the emphasis on programs for conservation, river improvement, and flood control.

Bottomland is undoubtedly the preferred habitat of raccoons and over much of the vast Mississippi basin is the best range available for numerous forms of wildlife. This paper is a contribution toward the management of river bottom lands.

Area Studied

This study was made in a tract of 2,175 acres locally known as Calhoun Point, generally typical of the larger flood plains north of the Ohio River. This somewhat triangular area lies immediately above the confluence of the Mississippi and Illinois rivers (Fig. 1), and is bounded by them on all sides except along the west. It is treated here as a unit of four square miles, a procedure probably contributing to the accuracy of the data, as a few raccoons may have been drawn from adjoining territory.

The area is under the jurisdiction of the War Department and is affected by the river improvement and flood control program. It is now formally designated as the Pere Marquette Wildlife Experimental Area, and is a study center for the Illinois Natural History Survey.

Calhoun Point includes many subtypes of habitat, the most obvious being the margins of large rivers, sloughs, small lakes, marshes, borrow pits,

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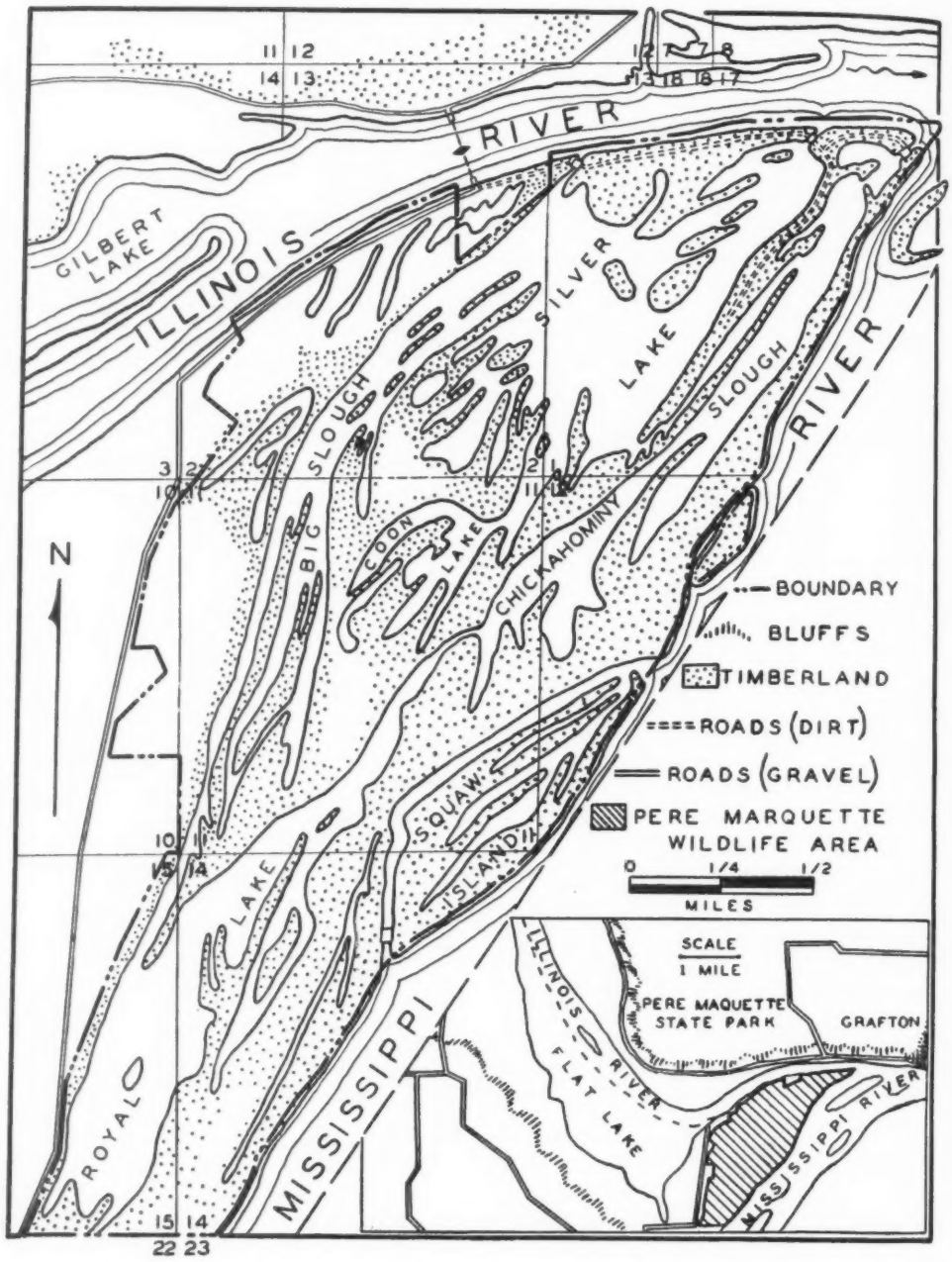

Fig. 1. Generalized post-flooding map of Pere Marquette Wildlife Experimental Area and vicinity, showing the extent of flooding. Much of the area shown as water is covered by dead timber still largely standing.

flooded woodland, forested ridges, brush land, cut-over land, fallow land, and levees. The water varies from muddy to almost crystal clear; the influx from the silt-laden Mississippi and Illinois rivers is noticeable in the connecting sloughs for only a few hundred yards from the parent streams, except at flood stages, such backwaters being progressively clarified by sedimentation. The present level is stabilized by a large navigation dam across the Mississippi River at Alton, Illinois, about 15 miles downstream. The maximum difference in land elevation on the area is about nine feet, on only two or three ridges.

Alluvial soil and flood plain forests characterize the area. From the muck in swamps to the sand beaches along the rivers and the loam formations on the highest ridges there is a comparable variation in the flora. Cottonwood (*Populus* spp.), willow (*Salix* spp.), white elm (*Ulmus americana*), soft maple (*Acer saccharinum*), hackberry (*Celtis laevigata*), and sycamore (*Platanus occidentalis*), are the principal trees along the river banks. On lower and wetter inland sites, elms and maples are more common, and on the lowest forested areas nearly pure stands of soft maple are found. Dense growths of water privet (*Forestiera acuminata*) and buttonbush (*Cephalanthus occidentalis*) grow along the former, but now flooded, shorelines and many of the larger privet and buttonwood shrubs are still living. On the inland flats and slough banks pecan (*Hicoria pecan*) hawthorn (*Crataegus* spp.), and persimmon (*Diospyros virginiana*) are common, the last often in colonies of 20 or more trees. Mulberry (*Morus rubra*) is plentiful on some ridges. Acorn and nut-bearing species are scarce except on the highest ridges, where pin oak (*Quercus palustris*) is abundant. Burr oak (*Q. macrocarpa*), scattered white oak (*Q. alba*), and shagbark hickory (*Hicoria ovata*) are other mast producers. Water locust (*Gleditsia aquatica*) and white ash (*Fraxinus americana*) are scattered widely. There are no beeches. This bottomland type is distinct from the cypress-tupelo gum-sweet gum types in the southern tip of Illinois and southward.

Vines are abundant on some sites to the point of killing trees. The most common are wild grape (*Vitis* spp.), but trumpet-flower (*Tecoma radicans*) and moonseed (*Menispermum canadense*) overrun other vegetation in places. The forest floor is covered chiefly by poison ivy (*Rhus toxicodendron*), wild rye (*Elymus canadensis*), pokeweed (*Phytolacca decandra*), false nettle (*Boehmeria cylindrica*), and several sedges (*Carex* ssp.). Poison ivy is particularly luxuriant, 5 or 6 feet tall in many places, and so thick that one can see only a few yards among its upright stems.

About 150 acres of fallow land along the west end now supports a rank growth of ragweed, trumpet-flower, dewberry, blackberry, grasses, and composites, being bounded on all sides by woods and sloughs. Some of this area was in corn as late as 1940.

Coincident with the river improvement program and the development of Pere Marquette State Park, three changes profoundly affecting the ecology of the area were begun in 1938. The Alton Dam raised the Mississippi River about 5 feet at Calhoun Point, flooding about 600 acres of timber and vastly increasing the acreage of shallow water.

The best pin oak timber was cut from about 200 acres near the center of the area; and about 60 acres was cleared, and now is mostly flooded, along the Mississippi and Illinois shorelines. A 5-foot levee, having no effect on water levels, was built along part of the cleared shoreline necessitating the excavation of several acres for fill near the junction of the bounding rivers.

The full effect of these changes on the animal life cannot yet be measured, but such information is not needed here because all the data, including fur catch records, pertain only to the second and third years subsequent to flooding, cutting, and clearing. Of the fur animals only the muskrats appear to have reacted appreciably to the environmental changes; raccoons showed great fluctuation in population, probably to causes unrelated to conditions on Calhoun Point. Data on these population adjustments are presented beyond.

About 80 years ago much of the best timber, and firewood for steamboat fuel, were cut. Many of the defective trees remain, chiefly huge, overmature or dying soft maples and some elms, sycamores, and oaks. The maples are multibranched, with wide-spread tops and short trunks 3 to 7 feet in diameter; invariably they are hollow and usually have one or more cavities suitable for raccoon dens. Limited sampling showed that cavities abounded, from 12 to 60 per acre. Some of those counted were too small for raccoons, but probably suitable for squirrels.

One important effect of the relatively stabilized level of clear water is the rank growth of submerged vegetation since 1938. Coontail (*Ceratophyllum demersum*) and in a few places leafy pondweed (*Potamogeton foliosus*) have practically filled some sloughs and have invaded flooded timber areas where hundreds of dead soft maple trees still stand. Duckweeds (chiefly *Lemna minor*, *Spirodela polyrhiza*, *Wolffia columbiana*, and *W. punctata*), varying in abundance from a broken film to a blanket more than an inch thick, cover most of the water area. It is difficult to propel a boat through the masses of floating and submerged vegetation. Such luxuriant plant growth indicates great fertility and probably presages early filling and conversion of the shallower sloughs to marshes.

Subsequent to flooding, cattail (*Typha latifolia*) and arrowheads (*Sagittaria* spp.) appeared, particularly along the borrow pits and cleared banks of the rivers and sloughs; muskrats now occur there in greatest numbers. There are scattered cattail clumps throughout the area, on both timbered and open sites, where the water table has been raised to within a few inches of the ground surface. Along the rivers and the more open sloughs, smartweeds (*Polygonum* spp.) and wild millets (*Echinochloa crusgalli* and *E. walteri*) have formed a dense band parallel to the water edge, undoubtedly originating from seeds washed up by wave action. Low flats may also support dense stands of smartweeds. Along the Mississippi and Illinois rivers during the last two years, sizable beds of longleaf and sago pondweed (*Potamogeton americanus* and *P. pectinatus*) have appeared on the flooded flats, due probably to nearly stabilized levels and clearer water during the late growing season.

FUR YIELD

Close estimates of the fur catch on the Pere Marquette area were obtained

for 1939–40 and 1940–41, and a poorer estimate for 1938–39, as follows:

Species	*1938–39*	*1939–40*	*1940–41*
Raccoon	35–40	170	60
Mink	20–30	45	40
Muskrat	50–75	225	260
Opossum	?	210	180
Skunk	?	25	16

The notable raccoon catch in 1939–40 of 42.5 per square mile, is believed to exceed any yield heretofore reported for a wild population on any comparable area. Yeager (1937) reported a higher yield from an 80-acre tract in Mississippi, but the population on any four-square-mile area there was much lower than on that under discussion. The Mississippi habitat was a well-wooded creek bottom, bordered by fields and pine-oak forest, and raccoons were concentrated largely in the lowland area. The Illinois catch of 170 animals should not, however, be taken as indicative of a normal population; it probably resulted from several factors: optimum or nearly optimum habitat, clearing, a "drift" or migration, heavy trapping, exclusion of night hunting, and unusually favorable trapping weather.

The general features of the Illinois habitat have been discussed, and its food resources are treated beyond in greater detail under Food Habits. The relation of the cleared area to the Mississippi and Illinois rivers and to Calhoun Point is shown in Fig. 1. Some 1,600 to 2,000 acres were cleared during the winter of 1938–39, on the west side of the Illinois River, where it might most effectively stimulate migration to the Pere Marquette area. How many raccoons moved over is unknown, but apparently several scores. One foreman kept a rough account of those seen and reported 22, including some killed or captured by laborers. Others may have escaped unseen. Several crews cleared the area now known as Flat Lake. The animals probably went both up and down stream, and it is impossible to estimate how many may have reached Calhoun Point. Some may have crossed the rivers after reaching the Point, despite the formidable widths of the Mississippi and Illinois, approximately one-half and one-fourth mile, respectively. More likely most of them found the habitat too favorable to leave and the population was gradually concentrated as clearing progressed. With this influx an appreciable number of breeding females probably was added suddenly within a few weeks of the mating season and produced litters not properly a part of the population. Breeding and maternal duties may thus have influenced the localization of raccoons which otherwise would have departed; and the offspring of such females were almost certainly held for a limited time by the influence of the home range.

Traveling or "drifting" raccoons, going downstream between the great rivers, would ultimately reach Calhoun Point, the "toe of the boot," comparable to the constriction of a migratory bird flight through a narrow funnel as at Point Pelee on the north shore of Lake Erie. Accumulations of drifting raccoons, finding excellent food and cover, would be limited only by overcrowding. Intra-specific tolerance in raccoons (as in most species) is not well understood, but probably varies with the character of the habitat. Raccoons are relatively gregarious, and probably tolerate comparatively high population densities. This concept is well supported by the present data. In any event, animals reaching this superb habitat probably

were not influenced by any special pressure, social or otherwise, to depart—a condition adding a cumulative quality to the drifting principle, which for ages has had its normal effect on the population.

The area was heavily trapped in 1939–40 by 35 men using an estimated 400 traps. From the opening day, November 15, to about December 20, the weather was almost perfect for the local methods of blind sets on logs and baited sets in shallow water; both of these types of sets are ineffective in freezing weather.

The foregoing combination of circumstances, plus the almost complete absence of night hunters (it is now difficult to follow dogs through the flooded areas), account for the unusual raccoon catch.

The take of 60 raccoons in 1940–41 is believed to be more nearly indicative of the normal population. Even this represents a yield of 15 raccoons per square mile. Trapping during the second year was scarcely as intensive as in the first. Clearing had little influence on 1940–41 numbers, since only a small acreage was involved. Thus, the 1940–41 catch may be within the limits of the annual expectation.

We hesitate to use the catch data for 1938–39, although three trappers were more or less in accord concerning it. It appears to be a reasonable estimate of the fur yield in the first season after flooding. Very little 'coon hunting was done on the area during that season, but for many years previously Calhoun Point had been rated an excellent hunting ground. Over-hunting prior to 1938–39 may have accounted for the comparatively small number of raccoons in that year. The small catch of muskrats, taken so soon after the approximate stabilization of the water level and before the development of marsh conditions, requires no comment.

The exact raccoon population is not known. The writers believe that about 80 per cent of the animals were removed in 1939–40, and about the annual increase of the remainder plus some drifting individuals were taken in 1940–41. These assumptions would indicate a population of 212 and density of 53 per square mile in the autumn of 1939. On this basis, 42 breeders remained after the trapping season; if half of them were females, an average mature litter of three is indicated. This would seem to be a reasonable and probably conservative appraisal of the population.

There is little of special interest in the catch of other species. The number of opossums for both years was high, with the effect of particularly heavy trapping in 1939–40 seemingly apparent in the catch for the succeeding year. The figures given are of those caught; not all were pelted, some being killed and discarded because of low fur value. Some were released and possibly trapped and included a second time in the estimates. Practically all were taken incidentally to trapping for raccoon and mink, as log and shallow-water bait sets are excellent for opossums. The slight decrease in mink in 1940–41 may have resulted from heavy trapping during the previous year. A considerable mink population still occurs on the area. Increase in the muskrat catch is to be expected with improvement in the marsh habitat, and higher prices for their pelts probably influenced the catch in 1940–41. Skunks are not abundant on Calhoun Point, be-

ing found mainly on the highest pin oak ridges. Both red and gray foxes occur, with the red predominating, but none was taken by trappers.

FOOD OF RACCOONS

The study of food habits by fecal analysis has been discussed by Swanson (1940) and used in many investigations of mammalian food, but only by Dearborn (1932), Giles (1939, 1940), and Hamilton (1940) for the raccoon. Studies of raccoon foods by Whitney (1931) and Hamilton (1936), were based on the visceral contents of animals taken by traps or dogs. These are summarized in Table 1. The Iowa study is the only one giving the year-around foods. The Michigan study probably is representative of summer foods in the Lake States. The raccoon's food habits have been studied most intensively in the northeastern states, by excellent investigations during the summer and the fall and winter in New York, and a qualitative report for the latter seasons in Connecticut and adjacent states. The present work is the first with specific data on the important river bottom habitat.

Table 1 confirms the general belief that the raccoon is omnivorous. As Hamilton (1940) says, " . . . animals, within limits, feed upon whatever is most easily obtained." Corn, fruit, crayfish, and insects furnish the bulk of the food, but to what degree the importance of these items is due to preference or availability we do not know. None of the above studies or that here reported gives complete food relationships, even for the seasons indicated, but Dearborn, Hamilton, and Giles (1940, fall) derived their information from good samples, and probably are representative for their regions. Giles' fall data for 1939 and 1940 show wide variation in quan-

Table 1.—REPORTED STUDIES OF RACCOON FOODS.

Season, Year, State, and Investigator	Materials		Vegetable: Animal Food Ratio Per Cent by Volume	Most Important Foods, as Percentage of Total Bulk																				
	Scats	Viscera		Corn	Corn and oats	Buckwheat	Cherries	Cherries-berries	Fruits-berries	Other fruits	Silky cornel	Raspberries	Grapes	Hackberries	Acorns	Beechnuts	Hickory nuts	Apple	Grass	Crayfish	Insects	Muskrat	Mice, shrews	Earthworms	Totals
Spring																								
1940, E. Iowa, Giles	41	—	54–46	5	—	—	—	—	—	—	—	—	—	—	—	—	11	—	37	8	35	—	—	—	96
Summer																								
1932, Lower Mich., Dearborn	500	—	32–68	—	20	—	—	12	—	—	—	—	—	—	—	—	—	—	—	59	5	—	—	—	96
1940, E. Iowa, Giles	44	—	69–31	13	—	—	—	—	—	—	—	32	—	—	—	—	4	—	—	—	26	—	—	—	75
1940, New York, Hamilton	163	—	80–20	7	—	—	38	—	—	—	27[1]	—	4	—	—	—	—	—	—	—	4	4	—	—	84
Fall																								
1939, Cent. Iowa, Giles	67	—	74–26	41	—	—	—	—	—	10	—	—	—	23	—	—	—	—	—	25	1	—	—	—	100
1940, E. Iowa,[2] Giles	272	2	85–15	85	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	10	—	—	—	97
Fall and Winter																								
1936, New York, Hamilton	—	130	74–26	8	—	16	—	—	11	—	—	—	—	—	6	14	—	14	5	2	7	—	8	8	99
1931, New England, Whitney[3]	—	128?	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Winter																								
1940, E. Iowa, Giles[4]	6	—	79–21	79	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15	—	—	—	—	94

[1] *Cornus anomum*, a shrubby dogwood.
[2] Aug. 11 to Dec. 7, includes some summer foods.
[3] Data qualitative. "Corn, oats, nuts, wild cherries, apples, pears, grapes, crickets, white grubs and trout."
[4] "Post-winter," March 23 to April 16.

tity of an item (corn), and great variety in the kinds of food taken. His two study areas were less than 100 miles apart, but whether the variations in his findings were due to regional differences or to insufficient data is unknown. Hamilton and Whitney found many foods taken in moderate quantities, suggesting variety and probably excellence in the habitats of the animals. In Iowa it appears that raccoons would suffer if the corn crop failed, an unlikely possibility. All of these findings suggest considerable adaptability of the species to its various environments.

MATERIAL

The present study analyzes 419 raccoon scats (droppings), from the Pere Marquette area taken in 1939 and 1940. Each year one series was collected between October 5 and 12, and another between November 15 and 20.

Collected	*Number of scats*	*Volume in cubic centimeters*	
		Total	*Average per scat*
Oct. 10–12, 1939	80	3,356	41.9
Nov. 16–18, 1939	110	5,901	53.6
Oct. 5–10, 1940	115	5,156	44.8
Nov. 17–18, 1940	114	6,658	58.4
Totals	419	21,073	50.3

In 1939 the scats were not separated, but the number in October and November were recorded. They were spread on heavy paper for uniform drying. In 1940, each scat as collected was placed in a small kraft bag, and quickly dried on the sand jacket of a coal furnace. After drying each collection was boxed and labeled until studied.

In all four series, the scats were gathered from practically the same logs, stumps, and soil mounds, providing a high degree of uniformity to the collections. Hundreds of additional scats could have been taken from the many other logs and stumps in the vicinity. Most of the stations were on the ground or in water, but some were 10 feet or more above the ground. Some yielded many scats; thus one had 27, 12, 19, and 11 scats, respectively, at the four times of collection. This was on a 4-foot maple, long fallen and rather isolated from other logs and stumps; the butt was hollow and extended into a timber-bordered slough. Muskrats had used the barely flooded cavity in 1940 as a feeding platform. Other than in this instance, the numbers of scats afforded no index for estimating populations.

Stumps used by raccoons as defecation sites were on or near the cut-over and now flooded pin-oak flats. Soil mounds and other elevations were infrequently used, probably because of comparative scarcity. Circumstantial evidence, from young and thriving grapevines, persimmons, pokeweeds, and smartweeds, even to 40 feet above ground, suggested rather frequent use of crotches in huge dying or dead maples as sites, some certainly being in den trees. It appeared that large logs were preferred as defecation places; those near water certainly were used more than logs on ridges at some distance from water. The same logs and stumps did not always yield material at each collection, probably because of the great abundance of logs and stumps. Scats on logs surrounded by water two or three feet in depth and accessible to raccoons only by swimming, showed that the animals visit such places when foraging.

In all collections an effort was made

to gather only recent entire scats, but this was difficult in October samples when the longer interval between collections permitted more weathering and disintegration. The rate of disintegration is significantly affected by scat composition. When the remains of crayfish and small, rounded seeds such as those of pokeweed and grapes were present, it was often difficult to gather whole scats if much disintegration had occurred. The surface on which scats are deposited affected the collecting. The flat surface of large stumps facilitated gathering droppings entire, whereas on small logs the material often became dislodged, and fragments dispersed upon disintegration. On many occasions portions of scats were recovered by searching the ground below the logs. Seeds and other items lodge in bark crevices or decayed wood, making full recovery difficult. Often several scats are dropped in one place and cannot be separated into individual droppings. This difficulty was solved in part by placing the more homogeneous material in separate bags; but with appreciable doubt the entire mass was discarded.

Another difficulty was that of excluding opossum scats. Opossums are abundant on the area, take the same foods as raccoons, and apparently use logs with some frequency for defecation. Size was most helpful in determining the origin of material; shape, composition, and odor were of some aid, but often uncertain. In agreement with Giles (1940), the senior writer found that fresh raccoon scats possessed a characteristic odor, distinctly less offensive than those of opossums, but this difference is partly lost by drying and weathering.

In both years the average scat was of smaller volume in October than in November, mainly because of the different degree of disintegration in the two months. If those of November are considered as entire, those for October show a weathering loss of approximately 25 per cent. Possibly the larger average size of the animals producing the November material made some difference in the average scat volume.

The present collection (of 419) is exceeded by Dearborn's total (about 500), but appears to be the most intensive yet reported. These are compared in the following summary:

Area of study	*Scats and/or viscera*	*Average number per square mile*	*Studied by*
New England	128	?	Whitney, 1931
Lower Michigan	500	?	Dearborn, 1932
New York	130	?	Hamilton, 1936
Central Iowa	67	?	Giles, 1939
Eastern Iowa, 21 sq. mi.	365	17.4	Giles, 1940
New York, 3+sq. mi.	163	54.3	Hamilton, 1940
Illinois, 4 sq. mi.	419	104.7	Yeager and Rennels

The October collections in Illinois were made before the opening of the waterfowl hunting season, and the November collections several weeks subsequently. In 1939 the opening date was October 15, allowing a 5-week interval between the beginning of hunting and collection; and in 1940 this date was October 22, giving a 4-week interval. The effect of hunting on the dietary habits of raccoons will be shown in the succeeding section.

Table 2.—FALL FOODS OF RACCOONS ON PERE MARQUETTE WILDLIFE AREA, ILLINOIS (*all figures are percentages*).

Food	1939		1940				Totals
	Oct. 80 Scats	Nov. 110 Scats	October 115 Scats		November 114 Scats		419 Scats
	Bulk	Bulk	Occurrence	Bulk	Occurrence	Bulk	Bulk
Persimmon (*Drospyros virginiana*)	22.7	20.1	69.6	34.6	86.8	34.6	28.6
Pecan (*Hicoria pecan*)	18.0	27.3	26.9	4.0	52.6	21.6	18.3
Wild grapes (*Vitis* spp.)	23.2	21.4	50.4	18.6	46.5	10.0	17.4
Crayfish	7.8	.4	70.4	16.0	57.0	10.6	8.6
Insects	9.8	7.0	85.2	10.1	68.4	6.4	8.0
Pokeweed (*Phytolacca decandra*)	11.6	4.9	44.3	9.6	27.2	2.1	6.2
Birds	1.1	13.5	7.8	1.7	27.2	3.9	5.6
Snails	.5	.1	40.9	1.5	68.4	9.3	3.4
Corn (*Zea mays*)	2.4	.3	7.8	2.8	3.5	.6	1.3
Fish	1.1	3.3	12.2	.3	5.3	.1	1.2
Mammals	1.1	1.4	3.5	.1	4.4	.3	.7
Fungi	.1	—	.9	tr	8.8	.3	.1
Greenbrier (*Smilax* spp.)	.1	.2	—	—	—	—	.1
Nightshade (*Solanum* spp.)	.2	—	3.5	tr	1.7	tr	.1
Blackberries (*Rubus* spp.)	.2	—	—	—	2.6	tr	tr
Wild millet (*Echinochloa* spp.)	tr	tr	10.4	tr	5.3	tr	tr
Turtle eggs	—	—	.9	.5	—	—	tr
Smartweeds (*Polygonum* spp.)	—	—	12.2	tr	7.9	tr	tr
Rice cutgrass (*Leersia oryzoides*)	—	—	.9	tr	.9	tr	tr
Pondweeds (*Potamogeton* spp.)	—	—	—	—	1.7	.01	tr
Compositae spp.	—	—	1.7	tr	—	—	tr
Field bindweed (*Convolvulus arvensis*)	—	tr	.9	tr	—	—	tr
Rose (*Rosa* spp.)	—	tr	—	—	—	—	tr
Sorghum (*Sorghum* sp.)	—	tr	—	—	—	—	tr
Lespedeza (*Lespedeza serica*)	tr	—	—	—	.9	tr	tr
Wild morning glory (*Ipomaea hederacea*)	—	tr	—	—	—	—	tr
Unidentified seeds (2 sp.)	—	—	.9	tr	.9	tr	tr

Total volume of all traces about 0.2 per cent.

ANALYSIS OF THE FOOD

In this study the volumetric technique was used. The dried scat contents were separated and measured by species or comparable groups, in cubic centimeters under a uniform pressure. The frequency of occurrence could not be determined for foods taken in 1939, but for the 229 scats collected in 1940, this information was carefully recorded. Plant foods were identified at least to genera; animal foods are listed by class (Table 3) and with more detail beyond. Only certain insects, birds, and mammals were identified to species.

Vegetable matter constituted 72.4 per cent of the fall diet, and animal material 27.6 per cent. This included 5 important plants and 6 important animal groups, each constituting more than 0.5 per cent of the total fecal bulk. The 5 plant items aggregate 71.9 per cent, and the 6 animal groups 27.6 per cent, together 99.5 per cent of the total volume.

Plant Foods. Persimmons are the most important fall food, more than a fourth of the total. Despite considerable losses by flooding, they are still abundant on the area. During October a bushel or more of fruit lay on the

ground under some trees and as much or more was still on the branches. The crop was noticeably heavier in 1940 than in 1939. Persimmons were present in about the same quantities in the four scat collections. Persimmon seeds averaged about 55 per cent of the total fruit bulk, and the seeds appear to pass unchanged through the animals, indicating that slightly less than half of the bulk of the fruit is digested.

Pecans of a native, wild species are

Table 3.—FALL ANIMAL FOODS OF RACCOONS ON PERE MARQUETTE WILDLIFE AREA, ILLINOIS, 419 SCATS (*all figures are percentages*).

Food	Total Bulk 1939–40 (from Table 2)	1939		1940			
		Oct. 80 Scats	Nov. 110 Scats	October 115 Scats		November 114 Scats	
		Bulk	Bulk	Occurrence	Bulk	Occurrence	Bulk
Crayfishes	8.6	100	100	70.4	100	52.0	100
Insects	8.0						
Hornets (*Vespa maculata*)		46	34	—	—	—	—
Water bugs (Belostomatidae)		28	26	72.7	77	77.2	71
Water beetles (Hydrophilidae)		9	23	7.8	1	20.2	2
Ground beetles (Carabidae)		7	4	13.9	tr	3.5	3
Wasps (*Polistes* sp.)		2	2	—	—	—	—
Grasshoppers (*Melanoplus* sp.)		1	4	—	—	—	—
Leaf chafers (Scarabaeidae)		—	—	2.6	10	—	—
Limnophilid larvae (Diptera)		—	—	—	—	7.9	18
Stratiomyiid larvae (Diptera)		—	—	8.7	7	9.6	2
Miscellaneous insects		7	7	13.0	5	8.4	4
Totals		100	100		100		100
Birds	5.6						
Ducks (*Anas, Dafila, Aix*)		—	89	—	—	14.9	76
Cormorant (*Phalacrocorax auritus*)		—	7	—	—	4.4	tr
Cardinal (*Richmondena cardinalis*)		—	—	.9	6	—	—
Other song birds		100	1	6.1	9	3.5	tr
Chicken		—	—	.9	85	—	—
Unidentified birds		—	3	—	—	7.9	24
Totals		100	100		100		100
Snails (*Physa, Stagnicola, Helisoma*)	3.4	100	100	40.9	100	68.4	100
Fishes (Cyprinidae, Centrarchidae, Catostomidae)	1.2	100	100	12.2	100	2.6	100
Mammals	.7						
Fox squirrel (*Sciurus niger*)		100	65	.9	53	1.7	tr
Muskrat (*Ondatra zibethica*)		—	—	—	—	1.7	62
Cottontail (*Sylvilagus floridanus*)		—	—	.9	tr	.9	34
Mice and shrews (*Microtus, Blarina*)		tr	tr	2.6	47	.9	tr
Raccoon (*Procyon lotor*)		—	—	—	—	.9	4
Miscellaneous mammals		tr	35	6.1	tr	4.4	tr
Totals		100	100		100		100
Reptile: Turtle eggs	tr.	—	—	.9	100	—	—

important in the fall food. The nut is about one inch long, of excellent flavor, and in November beneath some trees two or three nuts per square foot may be found on the ground. The 1940 crop was smaller than in 1939, and ripened later. A severe storm on November 11, 1940, blew down nearly all of the nuts, giving maximum availability to the raccoons; many scats collected on November 17–18 were almost entirely of pecan shells. The bulk percentage was 21.6 in November scats as compared to 4.0 per cent for those collected in October. Thereafter peacans were available in gradually decreasing quantity into the winter. As to food value, no calorimetric analyses are available but certainly they are of high rank. Pecan nuts undoubtedly contribute much to the excellent condition of raccoons on the area in fall and early winter. Despite an appreciable mortality in the trees by flooding, hundreds still remain.

On the basis of fecal bulk, grapes appear to be almost as important as pecans in the fall dietary; the summer grape (*Vitis aestivalis*) and the frost grape (*V. cordifolia*) are most common. Remains of the fruits began to appear in July scats and were evident until November or later. Scats collected early in August but not included here, were almost entirely of grapes. From 60 to 70 per cent of the total fresh grape volume is seed and skin, most of which is voided. The food value of grapes to raccoons is unknown, but their year-around importance is probably greater than indicated in Table 2.

Pokeberry grows luxuriantly on cleared shorelines and on the better drained ridges, where it tolerates considerable shading. The fruit ripens in late August, and the small shiny black seeds appear in scats immediately thereafter. Pokeberry is quite sensitive to frost, but may be available in some years until November. It is clearly most used early in the autumn. Scats composed largely of these seeds are perhaps the most difficult of all to collect without wastage, since disintegration is rapid, and the small, flattened seeds are easily lost. It was often impracticable to collect pokeberry-seed scats entire, despite considerable care, and the species is therefore somewhat more important than indicated.

The slight use of corn is probably indicative of the abundance of natural foods on the Pere Marquette area. Previous work, especially that by Giles (1939, 1940), has shown the importance of corn to raccoons in agricultural habitats. Pere Marquette, even at the point of heaviest collections, is scarcely more than a mile from extensive cornfields, yet corn made up only 1.35 per cent of the bulk in autumn scats. This emphasizes the availability of other foods, and suggests that items such as persimmons and pecans may be preferred. October-collected scats contained several times more corn than those of mid-November, suggesting that the corn supply may decrease materially in this 6-weeks period, or pecans may tend to replace corn in the diet, or corn may be less attractive when cured. Its food value is undoubtedly high.

More than 20 additional plant items were quantitatively insignificant in the fall diet. Many may have been taken incidentally, such as, wild millet while the raccoons were feeding on crayfishes or snails; and field bindweed when taking insects or fruits. Greenbrier berries

are fairly common in October, and their low rating is somewhat surprising; possibly they are not attractive to raccoons. Nightshade is not abundant on the area. Sorghum and rose hips, and perhaps pondweed and smartweed seed, would probably be taken in larger quantity if other foods were lacking. The scarcity of blackberry remains is to be expected in the fall, but both blackberries and dewberries are known staples in the diet of Pere Marquette raccoons during late spring and early summer. Most of the fungi were gill-bearing types (*Agaricaceae*), and may have been taken incidentally.

Animal Foods. The food residues of animal origin (27.6 per cent by fecal bulk) are detailed in Table 3, where each animal food species or group is arranged under appropriate headings and expressed as the percentage of the total class or subclass bulk for each collection. This permits direct comparison of each species or group with all others represented and also gives some information on fluctuations in foods and the effect of hunting on the volume and kind of birds appearing in the fall diet.

Because of the extensive and widely scattered water areas present, it is not surprising that crayfishes rank first in importance in animal foods. They were taken in greater quantity in 1940 than in 1939, possibly because there was a larger crayfish population in 1940, some 600 acres of shallow water then having been present for three years instead of two. The wide variation in the amount of crayfishes in the two 1939 collections is not understood. Observations throughout the year indicate that crayfishes are important at all seasons except in winter. Because of the proportionately large area of shallow water suitable for certain species, it seems probable that they will increase in importance in the future.

A variety of insects was eaten; most common were water bugs (Belostomidae). Their increased volume in 1940 is likely for the reason offered in explanation of a similar trend in crayfishes. The baldfaced hornet was the main insect food in 1939, but it and one of the paper wasps (*Politses* sp.), was not detected in 1940, for reasons unknown. *Polistes* were particularly numerous on the area, and had hundreds of nests during the summer and fall, many of which were built over water in bushes or small trees, either living or dead. The nests were up to 10 inches in diameter and populated by 100 or more adult wasps. The presence of dead wood offering unlimited material for paper, and of thousands of cavities suitable for hibernation, probably explain the local abundance of these wasps. Other insect foods were water beetles, ground beetles, scarabaeids, fly larvae, and miscellaneous forms, all taken in small quantities.

Birds constituted 5.6 per cent of the fall food. Miscellaneous song birds made up practically all of the avian bulk in the October samples. In both of the pre-hunting series birds amounted to less than 2 per cent; in November scats they amounted to 13.5 per cent in 1939, but only 3.9 per cent in 1940. In both years, the post-hunting collections contained a larger volume of bird remains, mostly of wild ducks, being 89 per cent of the total avian food in 1939 and 76 per cent in 1940.

The differences in the two years probably are explained by the hunting con-

ditions that prevailed. Near one of the collection areas three shooting blinds were much used in 1939, but only slightly in 1940. The senior writer observed several hunting parties at these blinds, and saw much long-range shooting which probably resulted in heavy crippling losses to ducks; thick brush on two sides of the blinds added to the difficulties of retrieving. Several cormorants (*Phalacrocorax auritus*) were killed there in 1939, and between duck flights any bird in or near range was likely to be shot. These conditions affected the feeding habits of the raccoons and are emphasized here because of the many distinct scats containing feathers seen during November, 1939. The ducks eaten were mainly mallards, pintails, and wood ducks. Cormorant feathers were frequent in the November 1939 material, but in small quantities in only 5 scats the next year. Chicken remains composed the bulk of one scat in October, 1940. Practically all of the large bird remains must have been carrion.

Similar conditions probably prevailed near other blinds on the area, but were not detected because no collections were made there. Raccoons that live near such food-rich habitats, expecially if undisturbed by dogs and night hunters, may be content to range locally; such behavior is indicated here only by circumstantial evidence.

Snails (*Physa*, *Stagnicola*, and *Helisoma*) were a variable item of food and of no special significance except in November 1940. The abrupt increase in volume then noted was probably due to low water in the Alton Pool after October 1, when the level was dropped about 20 inches. This exposed several hundred acres of debris-covered bottom on which were multitudes of snails at the time of the October collection. Snails were then present in fecal material in quantities several times greater than in 1939 (perhaps in part due to a larger snail population), but were not present in the volume in which they appeared later in the fall.

Fishes were of little importance in the fall diet. The species most commonly taken were carp and various sunfishes. The former were probably discarded dead from the large number of nets set in the Mississippi and Illinois rivers. Some of the fishes likely were taken from shallow pools resulting from drawdown in the Alton Pool.

Mammals amounted to less than one per cent of the fall food, being eaten infrequently; besides mice and shrews the bulk of such matter was probably carrion. Fox squirrel remains appeared in scats of both years, but in only one in 1940. Most of the squirrels taken were likely those crippled or killed and lost by hunters, who subject the area to heavy hunting pressure after about September 1. The muskrat and raccoon hair may have been chewed off recently skinned carcasses on which bits of fur above the feet were left. Such carcasses, thrown away by trappers, are plentiful a few days after the opening of the trapping season on November 15. Collection on November 18 would allow time for the hair to appear in scats. Pre-season trapping is said to have occurred. Raccoons seem to be addicted to gnawing the feet of carcasses, including those of ducks and geese, a trait often reported by hunters, trappers, and others.

Turtle egg shells were the only reptilian material identified, being practically all of a scat collected in October, 1940.

A number of other things may have been eaten but so thoroughly digested as to be unrecognizable in fecal matter. Earthworms are one example of such food. They abound in the soil of some Pere Marquette flats, and probably are taken. Hamilton (1936) found that earthworms made up 8.4 per cent of the fall food of New York raccoons, as indicated by the contents of 130 fall and winter visceral tracts. In another study, however (Hamilton, 1940), using the fecal analysis method, he reported no trace of earthworms in 163 scats from the Montezuma Marsh in the same state.

Present observations permit a general statement on food succession throughout the year for raccoons inhabiting the Pere Marquette area. The main winter staples are carrion (probably largely from skinned fur animals), winter-killed fishes, mice, and corn. Late spring and early summer foods consist largely of mulberries, dewberries, crayfishes, and insects, followed later in the summer by wild grapes, blackberries, and corn. Wild fruits and nuts are clearly the most important raccoon food resource in the autumn. The seasonal use of key foods again emphasizes the basic importance of availability.

SUMMARY

The fur yield and fall foods of raccoons were studied in 1939 and 1940 on the Pere Marquette Area, a river bottom habitat of four square miles in southwest Illinois.

Trappers reportedly took 170 raccoons during the fall and early winter of 1939–40, a yield of 42.5 per square mile. Such high density was apparently due to the natural excellence of the habitat, its location between and just above the confluence of the Mississippi and Illinois rivers, and to extensive clearing a few miles upstream during the winter of 1938–39. In 1940–41 trappers reported a catch of 60 raccoons, believed to represent approximately the annual increase of a more nearly normal population on the four square miles of probably optimum habitat.

Four collections totalling 419 scats were made, one in each year before and another after opening of the waterfowl hunting season. The four collections were made from practically the same logs and stumps, and amounted to 104.7 scats per square mile.

The vegetable food was 72.4 per cent and animal food 27.6 per cent of the total fecal bulk.

Persimmons, pecans, wild grapes, pokeweed berries, and corn, in the order named, were the chief vegetable foods; crayfishes, insects, birds, snails, fishes, and mammals were the principal animal foods. The effect of availability, seasonal or otherwise, was clearly apparent in the quantity and kinds of food taken.

Scats collected before the opening of the waterfowl season contained much less bird material than those taken a few weeks subsequently. Pre-hunting scats contained no duck remains, but in the post-hunting series, remains of mallard, pintail, and wood duck were 89 per cent of the bird material in 1939, and 76 per cent in 1940. Long-range shooting and ineffective retrieving appeared to be largely responsible for the availability of ducks to raccoons.

LITERATURE CITED

CASE, H. C. M., AND K. H. MYERS. 1934. Types of farming in Illinois. Univ. Ill. Agr. Exp. Sta., Bul. 403: 226 pp., illus.

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LITERATURE CITED

CASE, H. C. M., AND K. H. MYERS. 1934. Types of farming in Illinois. Univ. Ill. Agr. Exp. Sta., Bul. 403: 226 pp., illus.

DEARBORN, NED. 1932. Foods of some predatory fur-bearing animals in Michigan. Univ. Mich., School Forestry and Cons., Bul. 1: 52 pp., illus.

GILES, LEROY W. 1939. Fall foods of the raccoon in central Iowa. Journ. Mammalogy, 20: 68–70.

1940. Food habits of the raccoon in eastern Iowa. Journ. Wildl. Mgt., 4: 375–382.

HAMILTON, W. J., JR. 1936. The food and breeding habits of the raccoon. Ohio Journ. Sci., 36: 131–140, illus.

1940. The summer foods of minks and raccoons on the Montezuma Marsh, New York. Journ. Wildl. Mgt., 4: 80–84.

SWANSON, GUSTAV. 1940. Food habits of the sharp-tailed grouse by analysis of droppings. Journ. Wildl. Mgt., 4: 432–436.

WHITNEY, LEON F. 1931. The raccoon and its hunting. Journ. Mammalogy, 12: 29–38.

YEAGER, LEE E. 1937. Naturally sustained yield in a farm fur crop in Mississippi. Journ. Wildl. Mgt., 1: 28–36.

REPRODUCTION OF RACCOONS IN MICHIGAN[1]

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The raccoon (*Procyon lotor lotor*) ranks high in many states as a fur-bearer, and more recently has been regarded as a desirable game animal for hunting with dogs. There is a growing need to know more about its habits and requirements. Literature on the raccoon indicates that the little known of its breeding habits and breeding potential pertains almost entirely to captives, although these matters are basic to well-directed management. A few casual observations are available concerning breeding in the wild.

This paper provides data on reproduction obtained in an intensive two-year management investigation. The work was done at the Swan Creek Wildlife Experiment Station of the Game Division, Michigan Department of Conservation, located in Allegan County, along the Kalamazoo River, in the southwestern part of the lower peninsula. Several thousand acres of flood-plain and much more adjacent, sandy, oak-covered upland are available there. The combination of habitats makes the region one of the best for raccoons in the state.

In these studies (February 1939–January 1941), 256 individual raccoons were handled, all taken in live-traps and from dens except for 6 from a chicken coop. All were ear-tagged and many were recaptured. Some were examined during every month of the year, but the majority were taken in spring and summer.

SEX RATIO

In a male the os penis is easily demonstrated by palpation; the external urinary opening is several inches anterior to the anus. On a female, the genito-urinary opening is within about one inch of the anus. An old hunter told the

[1] Joint contribution of Pittman-Robertson Wildlife Restoration Project 1-R of the Game Division, Michigan Department of Conservation and Michigan State College. Published by permission of H. D. Ruhl, Chief of Division. Assistance in the studies by B. T. Ostensen, Zoology Department, Michigan State College, is acknowledged.

writer that he could sex raccoons by differences in width of the rings on the tail, a method supposedly taught him by Indians. There seems to be no correlation of color markings with sex, or any criteria by which males and females can be separated without close examination.

In the present study there were 133 males and 123 females taken, a sex ratio of 108 males to 100 females. Among 89 adults, 41 were males and 48 females, and of 167 juveniles, 92 were males and 75 females. Bennitt and Nagel (1937) reported 171 males and 135 females (127 to 100) in 306 raccoons killed in Missouri. Of 132 sexed by Preble (1941) in Ohio during the 1939–1940 hunting season, 73 were males and 58 were females (126 to 100).

RELATIONSHIP OF SEXES

Seton (1929) says: "All the evidence there is goes to show that the raccoon is a monogamous animal," but cites no evidence. Whitney (1933) considers them polygamous, apparently from observing captives. Fur-breeders seem to agree that a male will mate with more than one female, and this was so with penned animals at the experiment station.

The present study indicates that raccoons in the wild are promiscuous. Sexually mature males and females generally den singly. During the mating season, the former travel from one hollow tree to another, apparently seeking receptive mates. Wood (1922) mentions tracking for miles raccoons that had travelled over the snow visiting other dens. The tracks he saw were likely those of males active during breeding season. Females have been found to go short distances from their dens at that time, but males are the real travellers.

Five females in estrum were examined in 1940, three each in separate dens. Another was an adult denning with two yearling males disturbed previously in another den, after which they had moved. Their situation should not, therefore, be considered indicative of normal behavior. The last female was a yearling found with a male of the same age. Upon recapture two months later she was neither pregnant nor lactating, indicating that the two were not a mated pair but were more likely litter mates of the previous year. Three additional females, two located during the breeding season but not examined and the third pregnant in May also were alone. Seven other females were in dens with their litters, unaccompanied by males.

Lone mature males have been found in dens at various times of the year and tracks of toe-clipped individuals provided further evidence that they lived alone. During the mating seasons of 1940 and 1941, two toe-clipped males were tracked in the snow. Figure 1 (*left*) shows the 1½-mile trail of adult male no. 694; on February 5, 1940 he visited several dens and probably mated with at least one female. On February 11, 1940, he was in the same territory and his trail was followed for nearly two miles. On the latter date, adult female no. 2037 was also found in a den, and her tracks were followed over the entire circuit she had made the previous night. These two animals met, possibly mated, then continued on their respective ways, she returning almost directly to her den (Fig. 1, *right*). Another adult male, finally located in a den on February 12, 1941, wandered about one mile

and visited eight hollow trees, six being den trees. He also was evidently seeking a mate or mates, but was unsuccessful during his observed travels (Fig. 2). Preble (1941) pointed out that the increased activity of males in winter indicates the onset of the mating season.

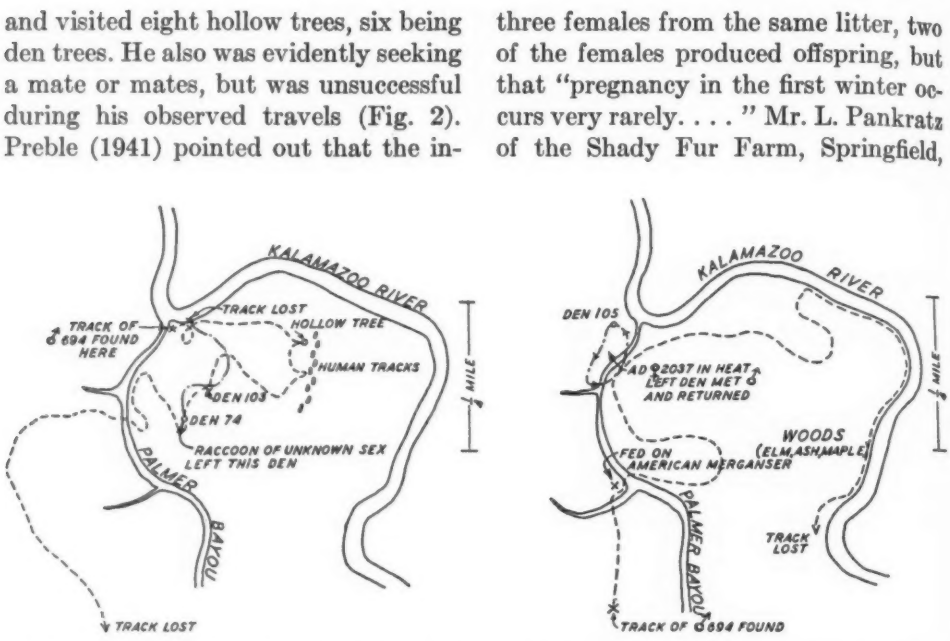


Fig. 1. *Left.* Activity of adult male (no. 694) and another adult of unknown sex during the night of February 5, 1940, in the breeding season. From tracks in snow at base of den tree No. 74, the raccoons might have bred there. *Right.* Activity of an adult male (no. 694) and adult female (no. 2037) during the night of February 11, 1940, in the breeding season. The male climbed several hollow trees during his travels. ----, path of male; -·-·-, path of female.

SEXUAL MATURITY

No information has been found in the literature as to the age when raccoons become sexually mature in the wild, and records are few for captives. Seton (1929) refers to a pet which gave birth to young when a year old. Bennitt and Nagel (1937) report that on a raccoon farm in Missouri six males observed from birth did not mate until two years of age, but 12 females mated at the age of one year. One yearling male was stated to have mated with females and litters resulted. Bissonnette and Csech (1938) report that of two males and three females from the same litter, two of the females produced offspring, but that "pregnancy in the first winter occurs very rarely. . . . " Mr. L. Pankratz of the Shady Fur Farm, Springfield, Minnesota, reports that yearling females produce litters, but that year-old males are not capable of breeding.

Males. In the present study evidence as to the age when males become sexually mature is meager and circumstantial, since there is no way of knowing whether or not a male has mated. Once a yearling male was found denning with a yearling female; she was in estrum but did not produce young that spring. Her failure may have been because the male was too young to mate successfully. Had he been in breeding condition, he probably would have denned alone, like adult breeding males. There is some evidence that the size of testes indicates the capacity of males to breed. Each

entry in Table 1 was obtained by measuring the scrotum in an animal with the testes descended. The testes of juveniles and yearlings were abdominal and had to be forced carefully into the scrotum for measurement. Those of adults had usually descended during the breeding season and remained there until April and May; during the remainder of the year they were more often in the coelom, but vary in position. The measurements show that yearling males tend to have smaller testes than adults until past the mating season (February and March). The gonads in most of them apparently did not attain adult size (about 30 mm. long) until the autumn of the second year, prior to which the animals possibly were not sexually mature.

Females. Examination of 28 females showed conclusively that some of them become sexually mature and breed when about ten months old and bear young when one year old. These were captured from dens or in traps when in estrum, pregnant, lactating, or with litters of young. The state of pregnancy was difficult to establish positively. The abdomen was palpated to feel embryos, but the abdominal muscles were usually held rigid by the animal and doubt usually existed as to the determination. The diagnoses in four of five was later confirmed upon recapture; two had litters, and two were lactating. The fifth was not rehandled.

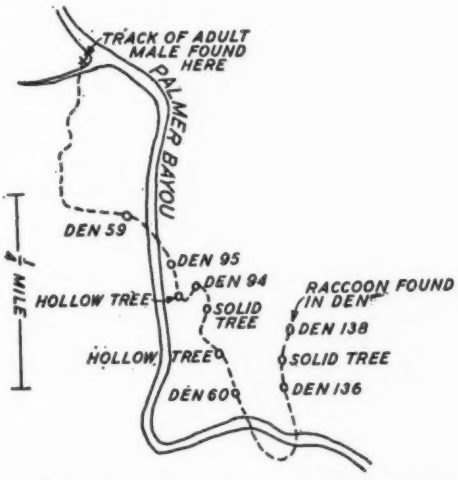


Fig. 2. Activity of an adult male on night of February 12, 1941, when he visited eight hollow trees. He was found alone in den No. 138 at the end of his trail.

Of the 28 yearling females, 15 produced young; 12 were lactating when examined between May and August and three were found with litters in dens. The ages of nine were known, having been marked the previous year as

Table 1.—LENGTHS OF RACCOON TESTES IN MILLIMETERS (*accurate to about 5 mm.*).

Age	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*
Adults		40		20	20	30	25	30	30	30	30	
				30	30	30	25	30				
				35	30		25	35				
							25					
							30					
							35					
Yearlings		15	15	20	20	30	20			30		30
		10	35	20	25					30		
				20	25							
					30							
Juveniles							10		10	10		
									10	20		
									15			

juveniles. The other six were classified as yearlings on the basis of weight, teeth, and other characters. Three of the remaining 13 animals may also have bred, but each was handled only once; one was not in estrum on February 3, another was in estrum on February 13, and the third was considered to be pregnant on May 17. Ten did not breed; they were neither pregnant nor lactating by May or later.

These data show that at least 15 (53.6%) yearling females produced litters. It is a matter of conjecture as to why the 10 individuals failed to reproduce. Of 27 adults all but one apparently in poor health were known to have mated, so it seems unlikely that there were not opportunities for all the yearlings to mate. The writer infers that the presence of a yearling male (probably non-breeding) with a young female might deter a sexually mature male from mating with her. In one instance a yearling female was found denning with a yearling male during estrum; later examination showed that she produced no young.

Several records give indications of the fecundity of females from year to year. One marked as a juvenile in 1938 produced a litter in 1939 and another in 1940. Four others were handled a sufficient number of times to learn that one which did not bear young as a yearling did so the second year, and three adults produced litters in two successive years.

REPRODUCTIVE CYCLE

Males. Ability to mate successfully apparently is not attained until the male is nearly two years old. The breeding cycle is likewise not well known. If testis size is significant, males are probably capable of breeding at all times of year after reaching maturity. The testes of four adult males in July, however, measured only 25 mm., smaller than the majority were during mating time and soon thereafter; in a captive male, the testes were 35 mm. long in March, but only 20 mm. in July. Whether the reduction is significant or not is unknown. From the behavior of captives, it appears that males are prepared to mate at any time.

Females. The vulva of a sexually quiescent female is not prominent. As the receptive period approaches, it becomes enlarged and turgid. During estrum the vulva is reddish and much swollen, the labia then protrude and are somewhat divergent. After mating, or when the animal is no longer receptive, the vulva gradually diminishes to normal size, and then is whitish in color.

The length of time from the onset of vulvar enlargement until a female becomes receptive apparently is between one and two weeks. On one captive swelling was first observed on February 23; a male was confined with her on March 8, when she was still receptive, and copulation followed. Probably she would not have accepted him more than a few days previously, since another female received a male during only three days. After copulation was observed, the male and female were separated. Twenty-one days elapsed before her vulva was down to normal size.

A male was noticed trying unsuccessfully to mount a female on February 10, 1940. Her vulva was somewhat swollen. Ten days later she was receptive to the male, and they were observed to copulate several times on three successive days. The vulva then was very turgid

and reddish. Thirteen days thereafter (March 6) the vulva was a bit enlarged but approaching normal. Gander (1928) also observed a pair to mate over a period of three days.

A yearling female that escaped in December, was retrapped on February 14, and held captive. She appeared to be in heat when caught, and the arrival of a litter on April 15 showed that she had mated in the wild about February 11. Her vulva was still greatly enlarged and turgid on March 3, 20 days after copulation. Five days later it was nearly normal but was not completely so until several days later.

From these observations it is apparent that from one to two weeks elapses from the onset of vaginal swelling until the female will receive the male. After the receptive period of about three days, three or four more weeks elapse before the vulva is again normal in appearance.

Mating season. The mating period seems to vary somewhat with latitude. In Connecticut and Massachusetts, Whitney (1933) says that raccoons breed during the last week in January. Hamilton (1936) states: "In New York mating normally occurs during the first half of February." According to Seton (1929), January or February is the mating season for captives in Ohio. In Oregon, where there are differences in seasons and temperatures from high altitudes to the lowlands, Bailey (1936) says that mating appears to be immediately after hibernation, from January to March.

The present studies indicate that most mating in southern Michigan takes place from the first week in February through the first week of March. The date of earliest breeding is based on a litter record in 1939. Judging from their size and development, the young appeared to have been born in the first week in April. The gestation period being about 63 days, the female must have copulated during the first week of February. Three litters, two to three weeks old, handled on May 23 and 24, must have been born the first or second week of May, which would place the mating dates of the females in the first week of March. An adult female handled on March 5 appeared to have recently passed the receptive estral period, possibly as late as March 1.

One adult female undoubtedly bred as late as May, and was parturient in July, probably as the result of a second estrum. When trapped on September 18 she was lactating profusely, and two juveniles, exceptionally young for that season, were taken the next day, one in the same trap and the other in an adjacent trap. All other females had ceased lactating a month before. The juveniles, whether from this adult or not, were surely born as late as July; they were small (4 lbs. 5 oz.; 4 lbs. 10 oz.). and retained their milk teeth until mid-October. Other young animals weighing as much were shedding their milk teeth in August. Other writers have had evidence of a few late matings. Hamilton (1936) mentions juveniles in New York that weighed less than three pounds in the fall and believed them to result from early summer breeding by females that failed to conceive during the regular breeding season. Similar observations were made by Whitney (1931) in Connecticut. Yearling females evidently do not breed late if they fail to do so in winter.

One yearling female probably mated in late March, since when handled on May 17 she appeared to be pregnant. As pointed out previously, pregnancy was correctly diagnosed for four or five individuals, which should support the validity of this record. This case is not considered indicative of the usual mating time of yearlings, because the male recaptured on February 14, 1939, held in captivity, and gave birth to young on April 18. Copulation therefore took place on February 11, if the gestation was the usual 63 days, and it must have taken place on or before February 14.

The data (Table 2) indicate that there is only one litter of young per female annually. The late brood as mentioned

Table 2.—DATA ON REPRODUCTION FOR 55 FEMALE RACCOONS.

	Copulation[a]		*Estrum*		*Pregnancy*		*Parturition*[a]			*Lactating*		*Postlactation*	
Age / *Dates*	*Unknown*	*Yrl.*	*Ad.*	*Yrl.*	*Ad.*	*Yrl.*	*Unknown*	*Ad.*	*Yrl.*	*Ad.*	*Yrl.*	*Ad.*	*Yrl.*
Feb. 1–Feb. 14	4	1	2	2									
Feb. 16–Feb. 28	3												
Mar. 1–Mar. 15	3		1	1									
Mar. 16–Mar. 31						1							
Apr. 1–Apr. 15							4		1[b]				
Apr. 16–Apr. 30						2	1	2					
May 1–May 15						1		2	1	5	1		
May 16–May 31						2				6	2		
June 1–June 15											1		
June 16–June 30										1			
July 1–July 15										6	1		
July 16–July 31										6	6		
Aug. 1–Aug. 15										1	5	2	3
Aug. 16–Aug. 31										2	1	3	1
Sept. 1–Sept. 15													
Sept. 16–Sept. 30										1[c]		1	
Oct. 1–Oct. 31												1	
Nov. 1–Nov. 30												1	

[a] Calculated from age of litters.
[b] Captive female littered on April 15.
[c] Unusually late litter (see text).

jority evidently breed at about the same time as adults.

The breeding data for 55 females are summarized in Table 2. Calculated copulation dates, records of females in estrum, and litter records indicate that most mating occurs in February and early March. One record shows almost the exact date on which a female copulated. This animal had been a captive but escaped in December, 1938, and having had her freedom for two months before mating time, her breeding activities should have been normal. She was earlier suggests that there may be a second estrum for adult females which fail to conceive in February or March, but available evidence shows that only one litter is produced. Bissonnette and Csech (1938) were able to obtain two litters from captive animals by artificial lighting of the pens which brought about first matings in December and a second in May or June.

Gestation. The only record on length of the gestation period in the wild is for the escaped animal mentioned previously; she was known to be pregnant at

least 60 days before parturition. The records in Table 2 indicate about two months between mating and birth of young, but afford no exact limits.

There are several records in the literature for the gestation period of captives. Hamilton (1936) and Seton (1929) both give 63 days. One animal observed by the writer gave birth to young at least 64 (or 66) days after the last copulation; the young were probably two days old when found. Gander (1928) observed a California raccoon (*Procyon psora californicus*) that was pregnant for 65 days after the last mating. The longest time is cited by Brown (1936), of a female becoming parturient 69 days from first coition.

Lactation. According to the literature, there is a difference in the number of teats possessed by female raccoons. Four pairs are shown on a raccoon killed near Toronto, Canada, in 1888, sketched by Seton (1929). Bailey (1926) in raccoons of North Dakota mentions two pectoral and two abdominal pairs, and of Oregon raccoons (1936) says there are three pairs—pectoral, abdominal, and inguinal. All of the 126 female raccoons in this study had three pairs—thoracic, abdominal, and inguinal.

The teats of an unbred yearling raccoon are about 1 mm. long, undeveloped, and flesh colored; they remain so if the animal does not breed. The teats enlarge in advanced pregnancy, become much larger after parturition and suckling, and usually are almost black. The color varies somewhat, being mottled in fleshy and darker hues on one lactating female. During lactation each teat is 10 to 15 mm. long, the proximal portion being a slight elevation 15 to 20 mm. in diameter. When lactation ceases, the teats diminish to small nipples about 5 mm. long, larger than before being suckled.

During the lactating period, milk could be obtained by gently squeezing and "milking." For a short time thereafter a yellowish or almost clear syrupy fluid was present, and later none. All fecund females lactated through July, but the majority had stopped by the end of August (Table 2); five were "dry" by mid-August. An exceptional animal still lactating on September 18 has been mentioned.

Table 3.—BIRTH DATES OF RACCOONS AND SIZE OF LITTERS.

Month of birth	*Young per litter*	*Authority*
April and May	3 to 6	Anthony (1928)
Early May	4 to 6	Audubon and Bachman (1851)
April and May	3 to 6	Cory (1912)
?	4 to 5(6)	Goodwin (1935)
April and May	3 to 7[a]	Grinnell, Linsdale and Dixon (1937)
?	5 or 6	Ingersoll (1907)
?	3 to 6	Kennicott (1858)
?	8[b]	Martin (1939)
April or May	3 to 6 (4 usual)	Seton (1929)
April and May	3 to 6	Stone and Cram (1902)
?	2 to 3	Sweeney (1905)

[a] Wild (embryos and litters).
[b] Captive.

The young evidently are suckled after they leave the den to accompany the mother in seeking food. The milk teeth of juveniles are not then replaced by the permanent teeth. This change occurs during August, when the females cease to lactate, a favorable adjustment of juvenile development whereby the animals have means to obtain and utilize solid foods when weaned from the milk diet.

Litters. Of the several references on the number of young in a litter and approximate birth dates (Table 3), only one is for animals in the wild. Grinnell, Linsdale and Dixon (1937) give records

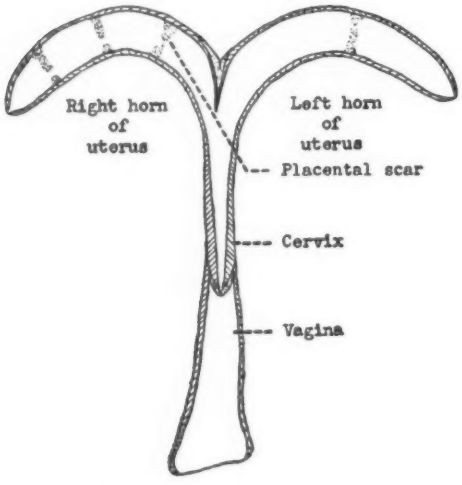


Fig. 3. Diagram of genital system of two-year old female raccoon, about four weeks after parturition. Scars of zonal placentae show that she gave birth to four young.

for the California raccoon (embryo counts and litter observations) of 3 to 7, and concluded that young are born in April and May.

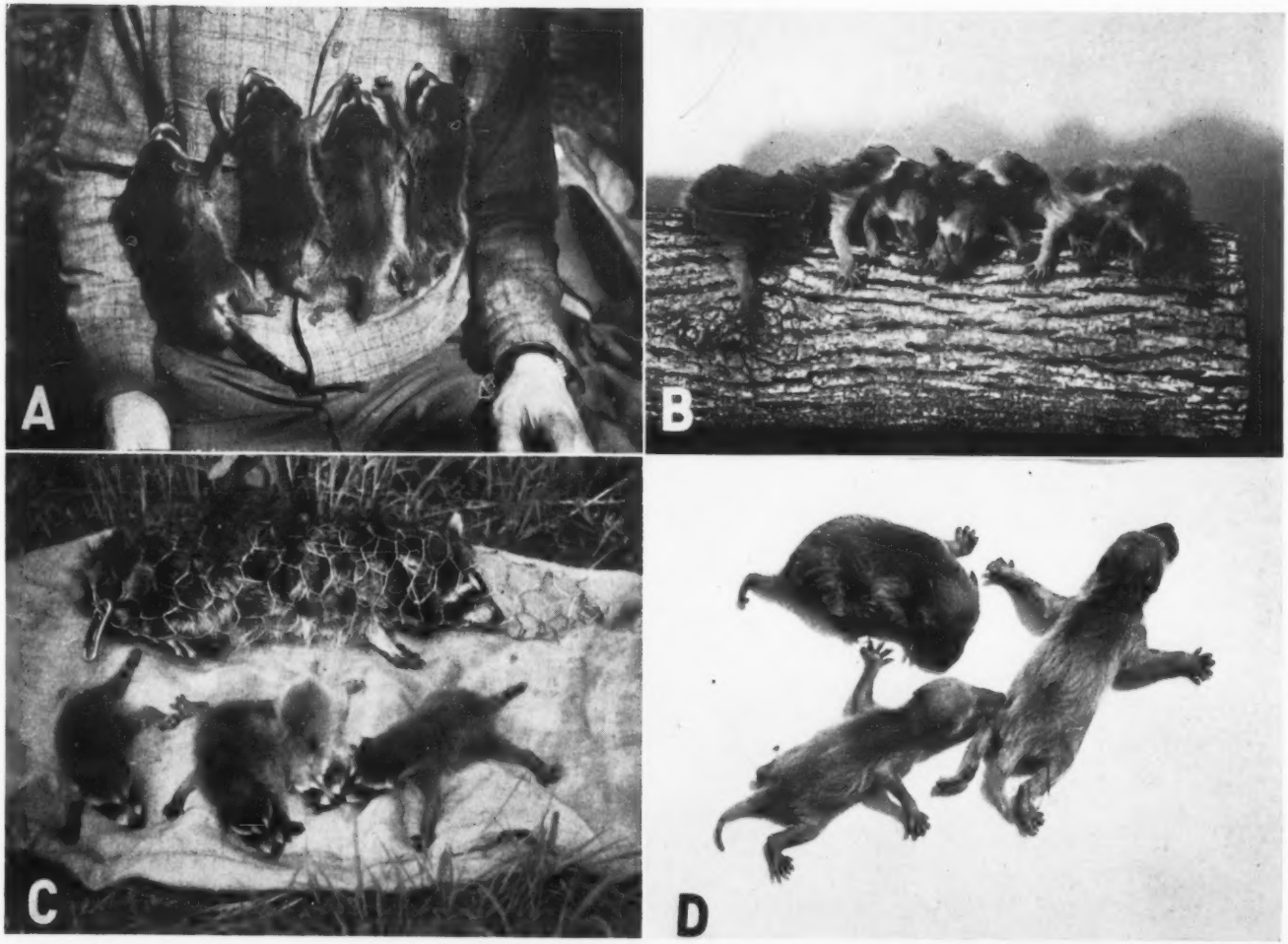
In the present study, ten litters, one to ten weeks of age, were examined in dens and a female autopsied on May 29, 1940, had scars of 4 recent placental attachments (Fig. 3). Judging from the age of the juveniles, all were born during April or the first half of May. The litters varied from 3 to 7, averaging 4 (Pl. 3*A*, *B*). One litter of two and another of three were born in captivity, the latter to a female which had escaped captivity and mated in the wild.

Records show that the litters of yearlings and adults are probably the same in size. Four wild adults had three and four each, and a captive only two. A wild yearling produced three, and a captive three.

In eight litters where all the young were handled, there were 14 males and 19 females, a sex ratio of 73.5 males per 100 females (Table 4).

Breeding potential. Data already presented indicate that (1) the sex ratio in this region is nearly equal; (2) approximately 50 per cent of the females bore young as yearlings; (3) one litter per year was produced thereafter; (4) it was exceptional for an adult female not to raise a litter; and (5) the average litter size was four. A figure representing the breeding potential of the species therefore can be postulated, of 4 to 1 per female or 2 to 1 per adult if all yearlings bred. Since 53.6 per cent of the yearlings actually bred, a correction must be made. First, however, another unknown must be established, the relative numbers of yearling and adult females breeding in a population. Intensive work in one area by trapping, den examinations, and tracking of toe-clipped animals, showed the ratio of breeding yearlings to adults was 50:50 (14 yearling females, 7 of which theoretically bred, and 7 adult females). The breeding potential therefore is 3 to 1 female or 1.5 to 1 adult. On this basis, neglecting all mortality, autumn populations would be 1.5 times greater than the annual breeding reserve.

Bennitt and Nagel (1937) arrived at the same figure (1.5) to represent the actual ratio of increment by any given autumn. They considered the average litter size to be four, but deducted one to allow for mortality and assumed that all young females begin to breed



Michigan raccoons. *A*. Average litter, 14 to 20 days old (May 23, 1940). *B*. Exceptionally large litter of seven, 10 to 15 days old (Apr. 29, 1940). *C*. Adult female (in wire handling cage) with litter of three and one adopted (palest) from another female. *D*. Captive-born litter of three on day of birth.

Michigan raccoons. *A*. Average litter, 14 to 20 days old (May 23, 1940). *B*. Exceptionally large litter of seven, 10 to 15 days old (Apr. 29, 1940). *C*. Adult female (in wire handling cage) with litter of three and one adopted (palest) from another female. *D*. Captive-born litter of three on day of birth.

when one year of age. Their deduction of one per litter balanced the allowance made in the present work for only 50 per cent of the yearling females producing, thus giving the same final figure. Their figure represents the ratio of *actual* fall increment and the present one the *potential* increment disregarding mortality. If raccoons in Missouri show the same tendency for approximately only one-half of the yearlings to breed, their figure would be reduced to 1.12.

Table 4.—DATA FOR 10 LITTERS OF RACCOONS IN DENS.

Date handled	*Age of female*	*Number of young*				*Approx. age in days*	*Estimated time of birth*
		Male	*Female*	*Unknown*	*Total*		
4-29-40	?	3	4	0	7	10–15	Apr. 2nd wk.
5- 3-39	Adult	1	3	0	4	21	Apr. 2nd wk.
5- 3-40	Adult	2	2	0	4	7–10	Apr. 4th wk.
5-10-40	?	2	1	0	3	7–14	Apr. 3rd–4th wk.
5-11-39	?	0	5	0	5	14	Apr. 2nd wk.
5-11-39	?	—	1	2	3	21	Apr. 3rd wk.
5-23-40	Adult	4	0	0	4	14–20	May 1st wk.
5-24-40	Yearling	1	2	0	3	14	May 2nd wk.
5-28-40	Adult	1	2	0	3	21–28	May 1st, 2nd wk.
6-14-39	?	1	2	1	4	60	Apr. 1st wk.

Table 5.—REARING DENS OCCUPIED BY LITTERS

Den number	*Kind of tree*	*Den height (feet)*	*Hole diam. (inches)*	*Hole to nest (inches)*	*Nest diam. (inches)*
63	Red maple	55	6½ × 3	42	12×11
66	Red maple	22	6½ × 3¼	36	10×10
100A	Red maple	46½	5½ × 3	37	12×12
136	Red maple	26	18 × 5	58	12×11
138	Red maple	21	5 × 3	42	14×12
59	White ash	23	6½ × 5½	20	13×10
75	Black oak	23½	50 × 5	0	15×12
129	Butternut	38	14 ×10	7	15×10
134	Amer. elm	21	57 × 6	34	13×13

Care of young. Most raccoons in Michigan are probably born in tree dens, this type of home being preferred where available. Ground holes are reportedly used when hollow trees are scarce. All ten litters examined by me in the Allegan region, where hollow trees are plentiful, were in trees. In Illinois, at least formerly, the usual retreat was a hollow tree (Kennicott, 1858). In Colorado Bergtold (1925) found a litter in a magpie nest but considered the site unusual. In Iowa, Indiana, and other states, raccoons den in caves and crevices of rocky outcroppings (Giles, 1940; McAtee, 1907) and undoubtedly rear young there.

Table 5 shows the size of nine dens containing litters. Most of them had small entrances and were relatively deep, affording good protection to the young. Two, however, nos. 75 and 129, were fairly exposed; in each there was a long opening in the trunk leading to the nesting cavity, the bottom of which was practically at the level of the opening. The smaller dens must have afforded little room for the litters, even when one-third grown. Den no. 63 (12×11 inches) contained litters of five and seven in successive years. Crowding in such a small cavity must soon force the

family to find a new abode. During the summer the usual type of winter and spring dens may no longer be utilized; the animals then rest or find refuge in trees with open, shelf-like cavities, in crevices among roots of the large bottomland trees, or in the heavy vegetation of marshland.

In keeping with the polygamous habits of the males, on six occasions an adult was with a litter in a den, each was a female. Around another den there was a perfect track register of mud, in which tracks of a toe-clipped female were the only ones present. All evidence at hand indicates that the female alone cares for the young. Bailey (1905) gives an interesting account of the care a female tenders her litter. From a hollow "some thirty feet up in the trunk," one youngster fell to the water below. The mother started to the rescue, but the little fellow got back to the trunk and began to ascend, and the female returned to the den. About half way up the youngster began to cry and stopped climbing. This brought the female down, and "taking a good hold of the back of his neck and placing him between her fore-legs so that he, too, could climb, she marched him up the tree and into the hollow." The writer also made an unusual observation on the care of young. One juvenile of a litter tagged in a den with an identified female on May 24, 1940, was found on May 28 with the litter of another female in a different den. The adopted animal was approximately a week to ten days younger than the original members of the litter, but he appeared to be healthy and well cared for (Pl. 3, *C*). It seems possible that the first female, in moving her young, (as all females did after being disturbed), inadvertently dropped this one in the den of the other female and then left it when she found the hollow already occupied. Whenever litters were found, the mothers usually issued a few growled warnings and then, if possible, retreated to a place of safety for themselves. One left the den and jumped 23 feet to the ground, going away uninjured. She later moved two of the three young, but deserted the third.

Juvenile raccoons are entirely dependent upon the female and apparently get no food other than milk until they begin to accompany her in search of food, when about ten weeks old. During intensive live-trapping and tracking studies in 1940 the first evidence of young travelling abroad was by capture of one in a trap on July 12; it had been tagged in a den and was known to be about 12 weeks old. The first trapped in 1939 was also taken on July 12. From that time until the females ceased lactating in mid-August, the young evidently obtained both milk and solid food. How long family companionship continues after the young are weaned is unknown, but observations indicate that by autumn the young go their own way. From November 25 to December 12, 1939, tracks crossing a road track register showed that most of the animals were travelling singly, although pairs of juveniles were common. One day, after tracks of two juveniles had been seen together, the two were found in a den. During winter the raccoons were usually found alone in dens, except for a few yearlings. Since many yearling females breed, it seems logical that they would no longer stay with the mother at that time. Evidently some young raccoons of this region become

independent in autumn and all are so by winter. Some writers, however (Wood, 1922), believe that a family remains together in the home den until the young are a year old. Such opinions may be based on reports by hunters of "treeing whole families" in the hunting season, somewhat later as the tail rings and dark facial mask became apparent, giving the animals a more "coon-like" appearance. Thenceforth the changes were less conspicuous as the animals grew to adult size and proportions. Replacement of the milk teeth by the perma-

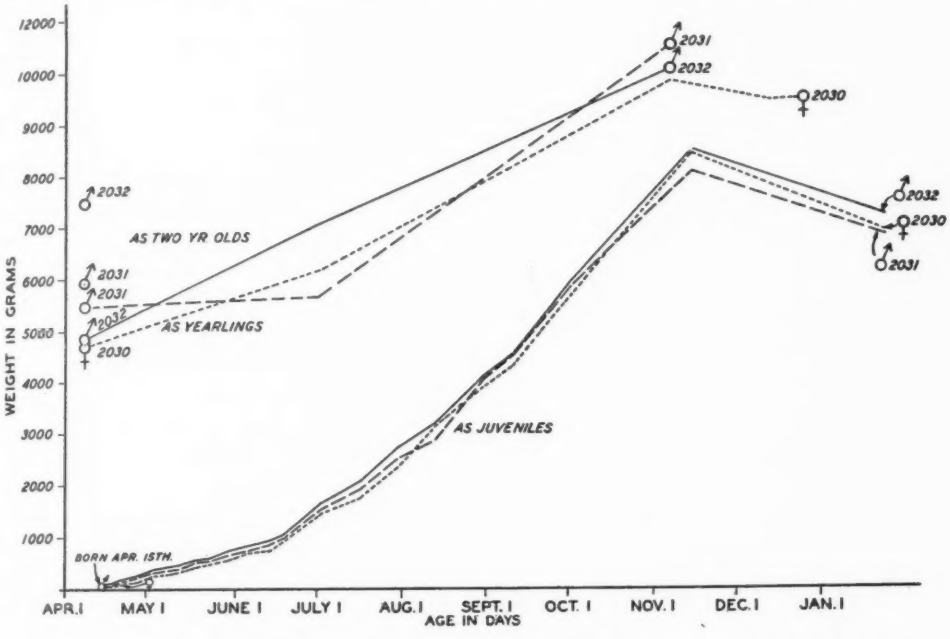


Fig. 4. Weight curves of three captive raccoons from birth until two years of age.

when the young may sometimes still be with the female.

Development of Young. The post-natal development of a litter of captives until seven weeks old was well described by Hamilton (1936). At birth, raccoons are well furred, have dark skins and well developed facial vibrissae, no rings on the tail, and the eyes and ears are closed (Pl. 3, *D*). In a captive litter the eyes and ears opened between the 18th and 23rd days. The lower incisors and canines then were erupting, but the upper incisors and other teeth emerged

nent set began at 16 weeks. Wild young were shedding the milk teeth during late August and early September, when 16 to 20 weeks of age, the incisors and canines being the first replaced.

The increase in weight of a captive litter of three during the first year and variations during their second and third years are shown in Figure 4. The average weight at birth was 61.7 grams. They grew slowly, and apparently were not fully grown in their second year. This also is true of wild animals as shown by 348 monthly weight averages

of juveniles, yearlings, and adults separated according to sex (Fig. 5). With one exception, adults, were somewhat heavier than yearlings for all corresponding periods of the year.

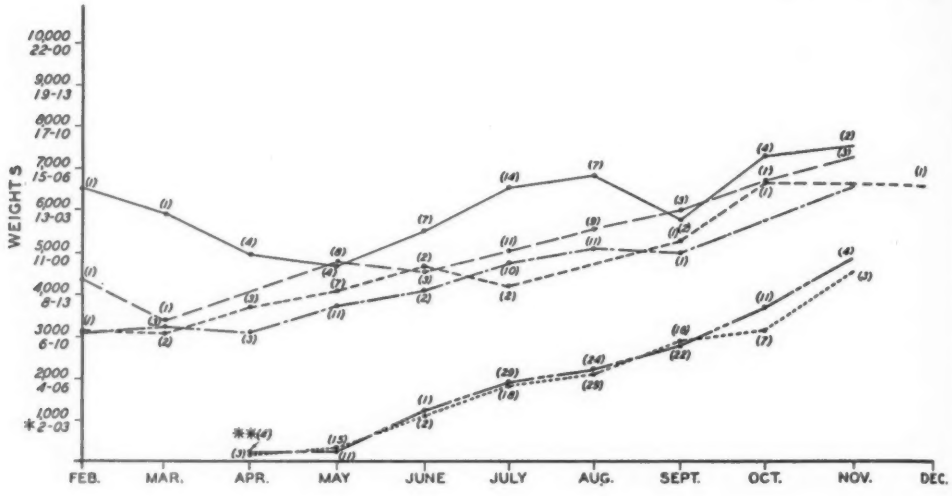


Fig. 5. Average monthly weights of 348 raccoons, juvenile, yearling and adult, handled in the wild; *, upper figures for weights are in grams, the lower in pounds and ounces; **, numbers of animals weighed are in parentheses.

adults: ———, males; — —, females;
yearlings: – – – –, males; — - —, females;
juveniles: — - - —, males: – – – –, females.

SUMMARY

1. The sex ratio among 256 raccoons was 108 males per 100 females. Accumulated evidence indicates that raccoons are promiscuous breeders; any male probably mates with more than one female in a season.

2. Males are probably not sexually mature by the first breeding season after their birth. Fifteen of 28 yearling females produced offspring, but 10 others had none during their first year of life.

3. Males seem to be able to copulate at all seasons. In females the onset of vaginal swelling occupies two to three weeks. Then they are receptive for about three days. After copulation three to four weeks elapse before the vagina becomes normal in appearance.

4. In Michigan the main breeding season is from the first week in February through the first week in March. A few adult females breed as late as May, evidently because of failure to conceive earlier. A female bears only one litter annually.

5. Young are born approximately 63 days after copulation; the majority arrive in April and May. The average number in 11 litters was four.

6. Lactation extends for about 14 weeks after parturition, but young leave the den when about 10 weeks old. Females alone care for the young.

7. Only about 50 per cent of the year-

ling females conceive, so that the breeding potential is 1.5 to 1 adult.

8. Juveniles shed the milk teeth during late August and early September, when 16 to 20 weeks old; the animals grow slowly, apparently not attaining full growth until at least the end of their second year.

LITERATURE CITED

ANTHONY, H. E. 1928. Field book of North American mammals. New York, G. P. Putnam's Sons.

AUDUBON, J. J., and J. BACHMAN. 1851. The quadrupeds of North America. New York.

BAILEY, VERNON. 1905. A biological survey of Texas. U. S. Dept. Agr., Bur. Biol. Survey, N. Amer. Fauna, **25**: 1–222.

1936. The mammals and life zones of Oregon. U. S. Dept. Agr., Bur. Biol. Survey, N. Amer. Fauna, **55**: 1–416.

BENNITT, R., and W. O. NAGEL. 1937. A survey of the resident game and furbearers of Missouri. Univ. Missouri Studies, **12**: 1–215.

BERGTOLD, W. H. 1925. Unusual nesting of a raccoon. Journ. Mammalogy, **6**: 280–281.

BISSONNETTE, T. H., and A. O. CSECH. 1938. Sexual photoperiodicity of raccoons on low protein diet and second litters in the same season. Journ. Mammalogy, **19**: 342–348.

BROWN, E. C. 1936. Rearing wild animals in captivity and gestation periods. Journ. Mammalogy, **17**: 10–13.

CORY, C. B. 1912. The mammals of Illinois and Wisconsin. Field Mus. Nat. Hist., Zool. Ser., **11**: 1–505.

GANDER, F. F. 1928. Period of gestation in some American mammals. Journ. Mammalogy, **9**: 75.

GILES, L. W. 1940. Food habits of the raccoon in eastern Iowa. Journ. Wildl. Mgt., **4**: 375–382.

GOODWIN, G. G. 1935. The mammals of Connecticut. Conn. Geol. and Nat. Hist. Survey, Bul. **53**: 1–221.

GRINNELL, JOSEPH, J. S. DIXON and J. M. LINSDALE. 1937. Fur-bearing mammals of California. Berkeley, Univ. Calif. Press.

HAMILTON, W. J. Jr. 1936. The food and breeding habits of the raccoon. Ohio Journ. Sci., **36**: 131–140.

INGERSOLL, ERNEST. 1907. The life of animals. New York, The Macmillan Co.

KENNICOTT, ROBERT. 1859. Quadrupeds of Illinois injurious and beneficial to the farmers. Rept. Commissioner Patents 1858, Agriculture. 35th Cong., 2nd Session Ex. Doc. **105**: 241–256.

MARTIN, E. D. 1939. Raccoon management and propagation. Ohio Conservation Bul., **3**: 4–5.

MCATEE, W. L. 1907. A list of the mammals, reptiles, and batrachians of Monroe County, Indiana. Proc. Biol. Soc. Wash., **20**: 1–16.

PREBLE, N. A. 1941. Raccoon management in Central Ohio. Ohio Wildlife Research Station, Ohio State Univ. Mimeo. release **161**: 1–9.

SETON, E. T. 1929. Lives of game animals. Garden City, Doubleday, Doran and Company, 4 vols.

STONE, WITMER and W. E. CRAM. 1902. American animals. New York, Doubleday, Doran and Company.

SWEENEY, Z. D. 1905. Indiana Commissioner of Fisheries and Game, Bien. Rept. Dept. of Game, 399–642.

WHITNEY, L. F. 1931. The raccoon and its hunting. Journ. Mammalogy, **12**: 29–38.

1933. The raccoon—some mental attributes. Journ. Mammalogy, **14**: 108–144.

WOOD, NORMAN A. 1922. The mammals of Washtenaw County, Michigan. Univ. Mich. Mus. Zool. Occ. Papers, **123**: 1–23.

FOOD OF THE RED FOX IN SOUTHERN NEW HAMPSHIRE[1]

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This report is based upon analyses of 313 droppings of the red fox (*Vulpes*) collected in southern New Hampshire from October, 1939 to October, 1940. The red fox is an important game and fur animal and of considerable interest to poultrymen and game managers, but there is little accurate information on its food in this region. Hamilton (1935) has studied its food in New York and New England, and Hamilton, Hosley and MacGregor (1937) in central Massachusetts.

For comparison the scats were divided into two groups, those collected from October 1 to April 30, called "winter" droppings, and the others from May 1 to September 30 or "summer" droppings. The major types of food by percentage frequency of occurrence were as follows:

Season	*Oct. 1–Apr. 30*	*May 1–Sept. 30*
Number of scats	206	207
Food		
Mammals	95	82
Birds	34	36
Insects	3	81
Vegetation	27	31
Fishes	1	2

Mammals were slightly more frequent in the winter scats and vegetation in the summer droppings, but the relative proportions for these two major types of food were nearly the same during the two periods. The only major change in diet was the high percentage of insects in summer. These findings are in contrast to those of Hamilton, Hosley, and MacGregor (1937) who found that during late summer and early fall in central Massachusetts, 86 per cent of the scats contained fruit, 53 per cent insects, 30 per cent mammals, and only about 4 per cent birds.

The mammals represented in the droppings, the number of times each item occurred, and their frequency percentage in each period are shown in Table 1..

Mammals

Field mice far exceeded any other item in the diet except insects during the summer period. That these rodents are a chief staple in the diet is thus reaffirmed. Deer mice formed a surprisingly small part of the diet (about 4%) both summer and winter when one considers their supposed abundance. Hamilton (1935) also found deer mice in only about 5 per cent of the stomachs he examined from New York and New England. Errington (1935), in studying the food of midwest foxes found only 3 deer mice in 46 stomachs (about 6%) and 104 deer mice in 1,175 scats (about 9%). Since deer mice are among the most abundant small mammals in most localities their relatively low frequency in the diet presents an interesting predator-prey relationship. The presence of a few lemming mice in the diet is interesting because they were previously considered to be scarce in the region.

[1] Contribution from the Biological Institute of the University of New Hampshire.

Snowshoe hares are not present in the region; the cottontail was the only rabbit represented. It ranked next to field mice in both winter and summer scats. In summer scats, woodchuck remains equaled those of the cottontail in importance but were absent from winter droppings. Of the winter scats 6 per cent contained remains of muskrats, 13 separate occurrences, but only one summer scat revealed traces of muskrat. Remains of livestock were found in 12 winter samples (6%) and consisted of wool, and horse or cattle hair with some hide. Undoubtedly this represented carrion; there was at least one horse carcass within the area of the collections.

Gray and red squirrels were present in the diet at all seasons, without significant seasonal difference in frequency of occurrence. Chipmunk remains were surprisingly infrequent and those of flying squirrel were found only once, in a winter scat. All of the insectivores present in the region were represented in the samples, but in low frequencies. Observations have shown the star-nosed mole to be much less abundant here than the hairy-tailed mole, but more of the former was taken. Remains of the star-nosed mole occurred six times during the entire year whereas the other species appeared but once and in a summer scat. The more frequent representation of the star-nosed mole probably reflects the greater surface activity of that animal. The short-tailed and the long-tailed shrews were taken sparingly although they are two of the most abundant local small mammals. The apparent distaste of the fox for shrews is affirmed by the findings of other investigators.

Skunk remains occurred five times in the winter scats and may have represented carrion since the fox is not known to prey on the skunk.

Table 1.—REMAINS OF MAMMALS IN 313 RED FOX SCATS.

Season	Oct. 1–Apr. 30		May 1–Sept. 30	
No. of Scats	206 Scats		107 Scats	
	Times Occurring	Frequency %	Times Occurring	Frequency %
Field mouse (*Microtus pennsylvanicus*)	130	63.1	56	52.3
Cottontail (*Sylvilagus transitionalis*)	54	21.3	14	13.1
Woodchuck (*Marmota monax*)	0	0	14	13.1
Muskrat (*Ondatra zibethica*)	13	6.3	1	.9
Livestock	12	5.8	0	0
Gray squirrel (*Sciurus carolinensis*)	10	4.8	4	3.7
Red squirrel (*Tamiasciurus hudsonicus*)	4	1.9	5	4.7
Deer mouse (*Peromyscus leucopus*)	9	4.3	4	3.7
Skunk (*Mephitis nigra*)	5	2.4	0	0
Short-tailed shrew (*Blarina brevicauda*)	4	1.9	3	2.8
Long-tailed shrew (*Sorex cinereus*)	3	1.4	1	.9
Star-nosed mole (*Condylura cristata*)	3	1.4	3	2.8
Hairy-tailed mole (*Parascalops breweri*)	0	0	1	.9
Lemming mouse (*Synaptomys cooperi*)	2	1.0	1	.9
Chipmunk (*Tamias striatus*)	2	1.0	2	1.9
Flying squirrel (*Glaucomys* sp.)	1	.5	0	0
Norway rat (*Rattus norvegicus*)	1	.5	0	0
House cat	0	0	1	.9
Unidentified	3	1.4	7	6.5

BIRDS

Bird remains occurred in 34 per cent of the winter scats and 36 per cent of those of summer but many were unidentifiable (winter, 22.3%; summer, 27%), being mainly quill bases, and feather and bone fragments. They may be reported as unidentified large birds (7%, winter; 5% summer), unidentified small birds (4% winter; 8% summer) and poultry remains (6% winter; 2% summer). The last is suprising because poultry would seem to be more exposed to fox depredation during the summer. Some of the winter remains of poultry evidently were carrion.

Ruffed grouse (*Bonasa umbellus togata*) were abundant during the period of collection but were only sparingly represented in the scats (3%, winter; 2% summer). These figures suggest that the red fox does not prey heavily on the grouse, although the opposite is believed by game-bird hunters. These figures are approximately the same as those presented by Dearborn (1932) for Michigan, by Hamilton (1935) for New York and New England, and by Hamilton, Hosley and MacGregor (1937) for Massachusetts. Some of the bird remains unidentified in this study possibly were those of grouse, but even small fragments of grouse feathers are readily identified by their distinctive patterns. Ring-necked pheasants were present in small numbers, but no remains were positively identified in any fecal sample. One winter dropping contained the remains of a crow. There were egg shells in about 5 per cent of the summer droppings and in 2.4 per cent of those from other seasons. Some were obviously fragments of poultry eggs, possibly refuse, and others were bits of smaller eggs, probably of ground-nesting birds.

OTHER ANIMAL FOOD

Insects were prominent in the diet during the summer, their remains being found in 81 per cent of the scats. This agrees with the findings of Hamilton, Hosley, and MacGregor (1937) of insects in 52.7 per cent of summer scats. Three-fourths of the New Hampshire occurrences were of grasshoppers and crickets, the rest of beetles. During the remainder of the year insects, mostly Coleoptera, had a frequency percentage of 2.8. The only other animal food in these scats was of fishes, the scales of the yellow perch in two winter scats and one of summer, and an otolith from a cod in a summer scat.

VEGETATION AND MISCELLANEOUS

Grass appeared in many fecal samples, but was recorded as food only when enough was present to indicate that it had been ingested purposely. Vegetable food was of almost equal frequency in summer and winter scats, but showed greater variety in summer scats; all winter occurrences were remains of apples, save for a quantity of grass in one scat. The items in summer droppings by percentage frequency, were as follows: blackberries, 14; apples, 12; fruits of wild sarsaparilla (*Aralia*), 7; grapes, 5; cherries (*Prunus serotina* and *virginiana*) 5; blueberries, 2; strawberries, 1; and grass, 1. Apples were prominent in the summer diet but less so than in winter. Hamilton (1935) noted the fondness of foxes for apples which they apparently dig from under the snow all winter long.

There was soil and detritus in vary-

ing amounts in most scats, and an occasional scat consisted almost wholly of fine soil or gravel. This may have been ingested incidentally with other food but such large amounts may indicate that it was taken for some special reason. Other items were paper, hemp rope, cotton twine, pieces of rubber, and lead shot.

This information on food of the red fox is preliminary and more studies are necessary before an adequate concept of the ecological position of the animal in this region can be obtained.

LITERATURE CITED

DEARBORN, NED. 1932. Foods of some predatory fur-bearing animals in Michigan. Univ. Mich. School For. and Cons. Bul., 1.

ERRINGTON, P. L. 1935. Food habits of mid-west foxes. Journ. Mammalogy, **16**: 192–200.

HAMILTON, W. J., JR. 1935. Notes on the food of red foxes in New York and New England. Journ. Mammalogy, **16**: 16–21.

HAMILTON, W. J., JR., N. W. HOSLEY and E. A. MACGREGOR. 1937. Late summer and early fall foods of the red fox in central Massachusetts. Journ. Mammalogy, **18**: 366–367.

DETERMINATION OF SEX AND AGE IN MUSKRATS

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Characters for determining the age and sex of muskrats (*Ondatra zibethica*) are not so apparent as in many other animals. In males and females the external genitalia are almost alike, the urethral papillae being similar in size and location, so that there often is difficulty in separating the sexes.

Age determination is possible by noting the general condition and degree of development of the internal genitalia, as described by Errington (1939), but this is not applicable with live animals and is too laborious when handling many dead specimens in a short time.

During recent trapping seasons in Illinois and Michigan the writers examined hundreds of muskrats on trap lines and at skinning houses and needed to determine the sex and age of many animals quickly. Since internal examinations were impractical, a more expedient method was sought. The method of age determination here described is based entirely upon characters of the external genitalia. It was developed independently by each author, but as the procedures and results were similar, it seems desirable to present them jointly.

The data for Illinois were taken between November 15, 1940, and January 15, 1941, and for Michigan between November 1 and January 31 of the same years. They represent late fall and early winter conditions in both states. Animals handled in Illinois were obtained from two adjacent lakes, Chautauqua and Rice. Those in Michigan were taken over the entire state.

SEX DETERMINATION

The most expedient way to determine sex is to note the presence or absence of a penis in the urethral papilla (Fig. 1).

If present, it can be exposed by pressing at the sides of the base of the urethral papilla. The vaginal orifice is at the base of, and posterior to, the urethral papilla; if closed, the orifice can be reopened by pulling the papilla forward and pulling posteriorly on the skin just anterior to the anus. In 8,107 individuals from Michigan, the males comprised 51.8 per cent, and in 2,090 from Illinois 48.8 per cent were males. The difference is 3 per cent between the two states but neither sex ratio is far from 50:50.

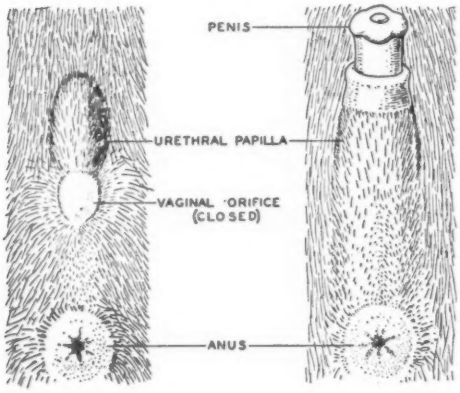

Fig. 1. External genitalia of subadult muskrats. *Left.* Female. Vaginal orifice closed by the vaginal membrane. *Right.* Male. The knob shaped tip of the penis results from tension by ligaments.

AGE DETERMINATION

Among females, adults were distinguished from subadults or yearlings by noting the condition of the vaginal orifice. In subadults (Fig. 1), this appears to be closed from the time of birth until just before the first breeding season, in the spring following their birth. In adults it appears to be open during most of the year. If a membrane forms over the opening, it is so thin as to break readily. In no adult female was the orifice entirely closed, but this might occur, especially in an individual which had missed one or more breeding periods. In subadult females the vaginal membrane is relatively thick, and considerable pressure is necessary to break it. The exact differences between the two age groups are difficult to describe, but become manifest when actually examining the animals.

The significance of vaginal membrane formation is not yet clearly understood in muskrats. It has been partly explained by Whitaker (1940) for *Peromyscus*, and by Baker and Ranson (1932) for *Microtus*. In those two rodents the vaginal orifice is closed from birth until the breeding season, when the vagina is open; during the anoestral period, however, the orifice is again closed by a thin membrane. Evidence of resealing of the vaginal orifice in muskrats was not observed in the specimens we handled.

Adult and subadult males are differentiated according to the size of the penis and the ease with which it can be pressed through the urethral papilla. The penis of an adult male is seldom less than 5 mm. or more than 6 mm. in diameter, is rather dark in color, and can be exposed readily. In a subadult male the diameter is 3 to 4 mm., the penis is more difficult to expose, and is lighter red in color. The extruded penis of an adult is longer than that of a subadult, but no definite measurements were made. The shape is also different, the penis being blunt and more or less rounded at the tip in an adult, whereas that of a subadult is knob-shaped (Fig. 1).

The validity of these characters was

checked in a substantial sample of individuals by comparing age determinations based upon external characters, with those based upon internal characters. The comparisons were not in complete agreement because the internal characters were confusing in some individuals, and in others the external characters were not very definite. The method, furthermore, does not facilitate the separation of age groups into categories other than adult and subadult.

AGE RATIOS

The age ratios for the muskrats examined are shown in Table 1.

The age ratios for the two adjacent lakes in Illinois were almost identical.

Table 1.—AGE RATIOS OF MUSKRATS.

	Subadults	*Adults*	*Totals*
Illinois			
Lake Chautauqua	691 (71.2%)	280 (28.8%)	971
Rice Lake	93 (71.0%)	38 (29.0%)	176
Totals	784 (71.1%)	318 (28.9%)	1,147
Michigan			
Zone 1	480 (72.2%)	185 (27.8%)	665
Zone 2	36 (76.6%)	11 (23.4%)	47
Zone 3	356 (68.7%)	162 (31.3%)	518
Zone 4	3,994 (63.6%)	2,287 (36.4%)	5,281
Totals	4,866 (64.7%)	2,645 (35.3%)	7,511

individuals difficult to classify were intermediate as to size and weight and constituted from two to five per cent of the total number examined. Considerations of weight and size with these questionable individuals often aid in proper classification, but alone are inadequate for determining age.

In employing this technique, the only difficulty was in differentiating the apparently intermediate muskrats, but errors from arbitrarily classifying such individuals will tend to cancel out. We believe the method to be sufficiently accurate for practical purposes. Efficiency in application will, of course, vary in degree with the worker's familiarity with muskrats.

This technique is of value only during the anoestrus or non-breeding period because the vaginal orifice is open just prior to and during the breeding season in all females, adult and subadult. The In Michigan they varied from 72.2 per cent for subadults in the north to 63.6 per cent in the south, for reasons not yet understood.

Assuming that trapping directly reflects population ratios, the average pair of adult muskrats produced only 4 to 5 harvestable muskrats during the 1940 breeding season. Preliminary life history studies indicate that 7 to 8 young per litter, and two litters a year are a conservative estimate of the muskrat's breeding potential. If the breeding potential is 14 young per pair of adults, and the harvest potential is only 4 or 5 per pair, then about 70 per cent are lost between birth and of the time harvest.

WEIGHTS

All muskrats examined in Illinois and a sample of those in Michigan were weighed (Table 2, Figs. 2, 3, 4). Adults from Illinois averaged 2.7 lbs. and those

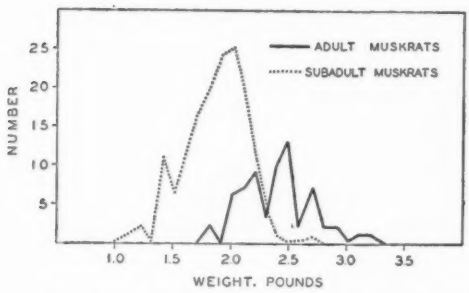

Fig. 2. Weight frequencies of 66 adult and 142 subadult muskrats examined in Michigan.

from Michigan 2.3 lbs.; the subadults of Illinois averaged 2.1 lbs. and those from

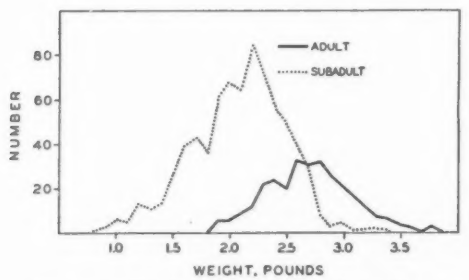

Fig. 3. Weight frequencies of adult and subadult female muskrats examined at Lake Chautauqua, in Illinois.

Michigan 1.9 lbs. These differences of 0.4 pounds in adults and of 0.2 pounds

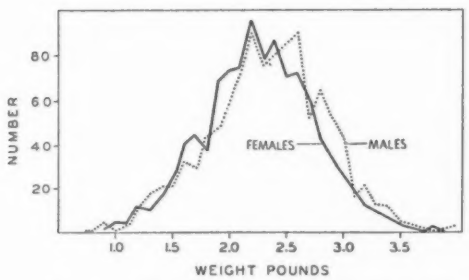

Fig. 4. Weight frequencies of male and female muskrats examined at Lake Chautauqua, Illinois.

in subadults appear significant, Illinois specimens being consistently heavier. It is not yet known whether this reflects differences in climate, geographic position, soil fertility, food supply, or the season when they were weighed. Most

Table 2.—WEIGHTS OF ILLINOIS MUSKRATS.

Weight, in pounds	*Rice Lake*		*Lake Chautauqua*	
	Subadult	*Adult*	*Subadult*	*Adult*
0.8			2	
0.9			5	
1.0			4	
1.1				
1.2	1		12	
1.3			10	
1.4			15	
1.5			25	
1.6	1		38	
1.7	3		41	
1.8	4		35	
1.9	8		59	5
2.0	9	1	66	5
2.1	9	1	63	8
2.2	4		81	11
2.3	10		52	21
2.4	4	2	55	23
2.5	8	4	48	19
2.6	8	4	38	32
2.7	4	5	28	30
2.8	7	3	8	31
2.9	5	5	2	25
3.0	5	5	4	20
3.1	2	3	1	16
3.2	1	4	1	11
3.3			1	7
3.4				6
3.5				3
3.6		1		2
3.7				0
3.8				2
Totals	93	38	691	280

of the Illinois muskrats were weighed between December 15 and January 15, and those in Michigan between November 1 and January 31.

As previously mentioned, considerations of size and weight might aid in determining the age of the infrequent intermediate individuals, but weight alone is not satisfactory for establishing age. The overlap in weights between large

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Left. Penis of adult male muskrat exposed by pressing at base of the urethral papilla. *Right.* Opened vaginal orifice of adult female muskrat at base of, and posterior to, the urethral papilla.

subadults and small adults (Figs. 2 and 3, Table 1) is too great for even a rough age classification.

The weight data secured at Lake Chautauqua were in sufficient quantity to illustrate weight differences between adult males and females (Fig. 2); the males there averaged 0.2 lbs. heavier than females. When tested statistically, this difference was found to be significant.

LITERATURE CITED

BAKER, J. R., and R. M. RANSON. 1932. Factors affecting the breeding of the field mouse (*Microtus agrestis*). Roy. Soc. London, Proc. ser. B, 110: 313; 112: 39; 113: 486.

ERRINGTON, PAUL L. 1939. Observations on young muskrats in Iowa. Journ. Mammal., 20: 465–478.

WHITAKER, WAYNE L. 1940. Some effects of artificial illumination in the white-footed mouse, *Peromyscus leucopus noveboracensis*. Journ. Exp. Zool., 83: 33–60

ADMINISTRATION OF BEAVER IN THE WESTERN UNITED STATES[1]

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We have long thought of the beaver as a great and depleted heritage, but today the West is already restocked with perhaps sixty per cent of the beaver it can potentially support—an estimated 324,000! Threatened by extermination only a few years ago, it already has passed that period in recovery where natural losses and poaching yearly destroyed almost all of the annual increase.

Today beaver are overflowing their homes in many western streams. In the winter of 1940–41 alone, nearly 54,000 were pelted under laws that provide for trapping beavers that threaten or actually damage irrigation and farms. In the same year several thousand more were livetrapped and transplanted to sites where they would become beneficial rather than harmful. We have indeed entered that era, long anticipated, when controlled utilization of beaver is a necessity rather than a hope.

Unlike game animals, beaver have an exceptionally high commercial value and are the easiest of all fur animals to exterminate. They are confined to waterways and their manner of life, building dams, canals, houses, and slides, with trails to freshly cut trees and shrubs, makes their presence easy to determine. Even inexperienced trappers can practically clean out several colonies in a few nights, and would garner enormous profits in return for this minimum of skill and effort, were it not for restraining state laws. Well prepared pelts brought as much as $45 each during the 1940–41 season, and the 54,000 then taken legally sold for more than $1,000,000. With a sound man-

[1] Data herein were furnished by game officials of the eleven western states which comprise the Western Association of State Game and Fish Commissioners and were assembled with help of the Federal Aid Division, U. S. Fish and Wildlife Service. Oscar H. Johnson was particularly helpful in this work.

agement policy, it is conservatively estimated that the western states could harvest a quarter million of beaver annually, to yield not less than $5,000,000 even with decreased prices.

Because of these large values and the ease of trapping, private interests have already, and in the future will increasingly, seek legislation to provide for opening the season on beaver to the general trapper. If such efforts become successful, the beaver is doomed and the conservation efforts of a half century will have been for naught.

It has become evident in recent years that the laws which were effective in restoring beaver now foster seeds of dissatisfaction and, in these days of beaver plenty, may lead to laws for its exploitation by the general trapper.

The present survey was undertaken to discover undesirable qualities in existing laws, to seek the most successful administrative practices, and to formulate a uniform plan for administering beaver in the West. If all of the states adopted a uniform policy embracing the more advanced practices, already tested and proved, such action would help markedly to defeat the efforts of private groups seeking the lawful exploitation of the beaver and also those now thriving on the traffic in "hot" beaver.

Table 1.—BEAVER IN THE ELEVEN WESTERN STATES, 1940–41.

State	Trapped Legally			Confiscated Pelts		Estimates		
	Number	Value		Number	Value	Pelts poached	Total population	Potential population
		Total	Average					
Arizona	83	$ 1,114	$13.79			100	4,500	8,000
California	94	896	9.53	7	$ 63	100	1,500	25,000
Colorado	12,000	195,000	16.25	300	4,000	6,000	40,000	90,000
Idaho	4,880	107,360	22.00	25	550	1,200	62,000	70,000
Montana	17,717	372,057	21.00	182	3,532	3,000	40,000	70,000
Nevada	No trapping in 1940–41					50	4,000	20,000
New Mexico	1,160	23,503	20.26	2	28	25	10,000	15,000
Oregon	2,286	60,394	26.42	14	140	400	50,000	85,000
Utah	2,202	39,807	18.08			200	15,000	30,000
Washington	2,568	51,855	20.19			1,200	57,000	86,000
Wyoming	10,946	244,643	22.35			2,000	40,000	65,000
Totals	53,936	$1,096,659	$20.33	530	$8,313	14,275	324,000	564,000

Approximately 58 per cent stocked.

CURRENT PRACTICES AND A MODERN BEAVER LAW

The survey revealed three factors that exert a major influence on beaver administration:

1. In ten of the eleven states there is no legal means for harvesting beaver except and until they threaten or actually cause damage.

2. Financial incentive for encouraging beaver on privately owned lands is almost lacking or actually prevented by most state legislation.

3. No satisfactory means has been evolved to stamp out interstate traffic in "hot" pelts.

THE 1940–41 TRAPPING SEASON

In 1940–41 practically all of the pelts harvested in the eleven western states were taken under "damage" laws. These are of two opposite types: either the state game department alone is authorized to remove offending beaver, or landowners are authorized to obtain permits from the department to remove beaver which are damaging or threatening their property.

Trapping by State Authorities. In four states only the game departments are authorized to remove harmful beaver, but landowners often request departments to remove beaver from their properties and all eleven states do some pelting and/or livetrapping, but only a few are authorized by law to share with landowners the income from sale of such pelts. In 1940–41, over 23,000 beaver were trapped and pelted by eight states. In no case did landowners receive any revenues although 95 per cent of the pelts were taken on private lands. The landowners are naturally not willing to suffer damage from the beaver and not interested in their management but wish only to have the beaver removed entirely.

The states received about $395,000 for these pelts. The cost of trapping, except for salaried employees, varied between $3.00 a pelt in one state to 50 per cent of the pelt value (paid to hired trappers) in others. In one case several prime dark "blankets" sold for $45.00 each and the trapper received $22.50 per pelt, a return far out of proportion to his efforts.

Table 2.—BEAVER TRAPPED BY STATE GAME AUTHORITIES, 1940–41.

State	Number	Percentages		Income (none to land owners)		
		of all trapped	on private lands	to State		to state trappers
				Per cent	Dollars	
Arizona	83	100	90	50	1,144	50%?
California						
Colorado	12,000	100	90(?)	100	195,000	50%
Idaho	4,880	100	75	73	78,630	27%
Montana	164	1 –	100	100	4,444	Salary
Nevada (1941–42)	118	100	100	57	1,572	43%
New Mexico						
Oregon	2,286	100	99	50	30,697	50%
Utah	378	17	72	50	6,834	50%
Washington	2,568	100	85	100	46,482	Approx. 10%
Wyoming	1,369	12.5	85	100	30,597	Salary?
Totals or Averages	23,846	70	88	75	395,400	40%

Trapping by Landowners. The laws of five states allow the landowner (or a private trapper as his agent) to take beaver damaging his property after first securing permission from the state game department. Over half of the beaver sold in the winter of 1940–41 were so obtained, mostly in two states. In the whole West they numbered about 30,000 beaver and brought an estimated $629,000. Of this sum the states received less than 10 per cent as pelt fees

and trapping permits from landowners. Such a low return is not enough for the state to maintain an adequate enforcement staff or men to advise and aid the landowners in managing their beaver so as to reap the greatest returns. It does not seem that the landowners realized any great income because, in turns with the landowner, there is no financial incentive to maintain a maximum of beaver on private lands and trapping volume is thereby lessened. Finally, the income of all three interested parties is lessened because the existing laws do not authorize an orderly harvesting under state control of

Table 3.—BEAVER TAKEN BY LANDOWNERS AND PRIVATE TRAPPERS, 1940–41.

State	Number privately trapped	Per cent of total trapped	Approx. value	Share of landowner and/or private trapper		Approx. return to state			Retained by trapper if acting for landowner
				Per cent	Dollars	Share of pelt	Trapping permits	Pelt fee	
Arizona	None								
California	94	100	$ 895	100	$ 895				75%
Colorado	None								
Idaho	None								
Montana	17,553	99+	368,613	100	368,613		$10,880	$ 8,701	50%
Nevada	None								
New Mexico	1,160	100	23,503	50	11,751	$11,751		1,160	25%
Oregon	None								
Utah	1,780	88	32,814	50	16,092	16,092			25%
Washington	None								
Wyoming	9,577	88	204,469	100	204,469			12,019	?
Totals	30,164		$629,663		$601,820	$27,843	$10,880	$21,880	

Total $60,603 to State.
State averaged only 9.6% of income.

most known cases, pelting was done by private trappers who refunded about $5.00 per pelt to the landowner-permittee.

Under most existing laws, therefore, the state, or the landowner, or both, receive a disproportionately small return. Regardless of who is authorized to do the pelting, private trappers do not realize as much as they would if the laws provided for a more equitable division of pelt returns, because the volume of trapping is needlessly small. In the absence of a management policy for *sustained yield*, there is a tendency to remove both the increase and the breeding stock from private streams when landowners are given permits, thereby lessening the prospects for future trapping. Alternatively, when the state does the trapping and is unable to share the returns with the landowner, there is no financial incentive to maintain a maximum of beaver on private lands and trapping volume is thereby lessened. Finally, the income of all three interested parties is lessened because the existing laws do not authorize an orderly harvesting under state control of all the surplus beaver on fully stocked areas.

WHO SHOULD PROFIT FROM BEAVER PELTING?

It is a fundamental precept of American government that the individual is free to exploit his environment as he chooses until his activities become detrimental to the common good. Trapping of beaver was long an inalienable right of the American citizen. The beaver disappeared because of its vulnerability, and one by one every state withdrew them by law from the field of unrestricted individual enterprise.

A half century of increasingly effective protection and a decade of intensive transplanting and management has been needed to bring the beaver back to abundance. During most of this long

period the state game departments, which protected beaver and spent large sums in protecting, livetrapping, transplanting, and conducting restoration studies, received no income from beaver. Unlike most other divisions of state governments, game departments, by policy and tradition, earn their own way. The cost of restoring beaver has been taken from funds gathered as fees for hunting, fishing, and trapping of other animals. When direct financial returns from beaver began to trickle in during recent years, the departments naturally welcomed an opportunity, figuratively speaking, to balance their long outgoing accounts against this animal. Today these returns in many states are considerable. If exploitation is prevented and the states become stocked to full carrying capacity, the annual harvesting of surplus beaver will soon be a routine measure and pelting will become a "big business." The annual harvest of beaver pelts may then be valued at several times the cost of all game department expenses. Under such circumstances retention of the entire income from beaver by a governmental department would appear in a different light.

Three groups other than the state must be considered in arriving at an equitable division of the income from beaver: (1) the landowner on whose property beaver are produced; (2) the general trapper who by personal initiative seeks income from catching and preparing fur animals for the market; and (3) the fur dealers who see in the beaver an exceptional opportunity for augmenting their business.

The landowners bear the entire responsibility of providing the beaver with places to live and food to eat. Beaver are a product of his land, like cattle and sheep, except that there would be no beaver on his land were it not for the protection and management afforded this wild species by the state. Big game mammals and game birds are also a product of land but they are maintained for recreational or aesthetic purposes and have no direct commercial value. Beaver, on the other hand, possess this direct and legal value and their harvesting is in no way related to recreation. Therefore the landowner who shares with the state the burden of raising beaver should likewise share any profits accruing from the harvest. The state stands to gain more financially by sharing pelt returns with landowners, as shown elsewhere in this paper, but this has no bearing on the present argument.

What is the state's obligation to private trappers who wish to trap on both public lands and private holdings? It would seem that there is only a secondary obligation. Beaver are not a natural resource which may be exploited by the individual without detriment to the good of all. The state's obligation is first to safeguard the resource, and then to protect the community and the individual property owner. Beaver have large potentialities for doing good or causing damage. The state, as the administrator, is responsible for so regulating beaver that they will yield maximum benefits and cause minimum damage. Finally, the financial returns to either or both the landowner and the state depend upon the care of the pelt. The state, therefore, is responsible for seeing that the persons permitted to trap beaver are reliable and well qualified.

After all of these responsibilities are discharged, if neither the state nor a qualified landowner is available to undertake trapping, the private trapper has a place in the program. Here again there are precedents and moral obligations to consider. Obviously all hope of

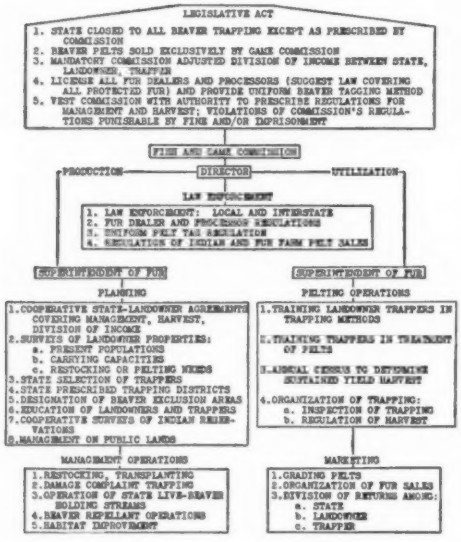
LEGISLATIVE ACT
1. STATE CLOSED TO ALL BEAVER TRAPPING EXCEPT AS PRESCRIBED BY COMMISSION
2. BEAVER PELTS SOLD EXCLUSIVELY BY GAME COMMISSION
3. MANDATORY COMMISSION ADJUSTED DIVISION OF INCOME BETWEEN STATE, LANDOWNER, TRAPPER
4. LICENSE ALL FUR DEALERS AND PROCESSORS (SUGGEST LAW COVERING ALL PROTECTED FUR) AND PROVIDE UNIFORM BEAVER TAGGING METHOD
5. VEST COMMISSION WITH AUTHORITY TO PRESCRIBE REGULATIONS FOR MANAGEMENT AND HARVEST; VIOLATIONS OF COMMISSION'S REGULATIONS PUNISHABLE BY FINE AND/OR IMPRISONMENT
FISH AND GAME COMMISSION
PRODUCTION
DIRECTOR
UTILIZATION
LAW ENFORCEMENT
1. LAW ENFORCEMENT: LOCAL AND INTERSTATE
2. FUR DEALER AND PROCESSOR REGULATIONS
3. UNIFORM PELT TAG REGULATION
4. REGULATION OF INDIAN AND FUR FARM PELT SALES
SUPERINTENDENT OF FUR
SUPERINTENDENT OF FUR
PLANNING
1. COOPERATIVE STATE-LANDOWNER AGREEMENTS COVERING MANAGEMENT, HARVEST, DIVISION OF INCOME
2. SURVEYS OF LANDOWNER PROPERTIES:
a. PRESENT POPULATIONS
b. CARRYING CAPACITIES
c. RESTOCKING OR PELTING NEEDS
3. STATE SELECTION OF TRAPPERS
4. STATE PRESCRIBED TRAPPING DISTRICTS
5. DESIGNATION OF BEAVER EXCLUSION AREAS
6. EDUCATION OF LANDOWNERS AND TRAPPERS
7. COOPERATIVE SURVEYS OF INDIAN RESERVATIONS
8. MANAGEMENT ON PUBLIC LANDS
PELTING OPERATIONS
1. TRAINING LANDOWNER TRAPPERS IN TRAPPING METHODS
2. TRAINING TRAPPERS IN TREATMENT OF PELTS
3. ANNUAL CENSUS TO DETERMINE SUSTAINED YIELD HARVEST
4. ORGANIZATION OF TRAPPING:
a. INSPECTION OF TRAPPING
b. REGULATION OF HARVEST
MANAGEMENT OPERATIONS
1. RESTOCKING, TRANSPLANTING
2. DAMAGE COMPLAINT TRAPPING
3. OPERATION OF STATE LIVE-BEAVER HOLDING STREAMS
4. BEAVER REPELLANT OPERATIONS
5. HABITAT IMPROVEMENT
MARKETING
1. GRADING PELTS
2. ORGANIZATION OF FUR SALES
3. DIVISION OF RETURNS AMONG:
a. STATE
b. LANDOWNER
c. TRAPPER

Fig. 1. A plan of organization for administration of beaver.

building up large, harvestable surpluses of many fur species on public lands in the future is dependent upon state regulation of trapping in accordance with sound management. There will probably always be too many trappers in proportion to the numbers of harvestable fur animals to allow all interested persons to garner a fair living through trapping. It will be necessary, therefore, for the state game departments to select and limit the number of trappers who may trap on public lands.

In allocating the use of public lands for grazing the basic objective is to stabilize local communities and adjacent private landowners. Itinerant stockmen have no place in this program. The same principle may eventually be applied to trapping rights, and public lands may be districted for trapping; inclusion of beaver among the furs that a bonded local district trapper may harvest would be logical and would lessen materially the size of trapping district needed to provide the trapper with a reasonable return to supplement his income from farming or other local occupation. This would enable more trappers to participate on public lands. Trapping is a distinctly seasonal occupation and there is little justification for it to become so lucrative on public lands that a trapper need have no other occupation.

Finally as to the fur dealer; his profits are derived from the spread between the price he must pay for pelts and that which he can obtain from the manufacturer. His primary interest, aside from a desire to procure prime pelts, is to buy at the lowest possible price. The better dealers offer a fair price for all pelts, but many unscrupulous and fly-by-night dealers take every possible advantage of inexperienced private trappers in states which do not require all pelts to be sold by the state. Sale of all beaver pelts by state game departments invariably results in better prices (often 100 to 400 per cent higher), and assures that the landowner, trapper, and state each receives a fair share. For this very reason, there is agitation by some fur dealers to obtain laws that would remove the control of trapping and sale of beaver pelts from the state and place such control in the hands of the landowner and the general trapper. An obvious obligation of

state game departments is to see that this control remains a state function.

DIVISION OF INCOME FROM BEAVER

If the income from pelting is to be divided among the state, the landowner, and the trapper, what should be the share of each? The question is debatable and various proportions are used in different states.

The state is entitled to a share that represents all costs connected with the administration of beaver, including law enforcement, overhead, investigations, and inspection service, and its share should also include a liberal margin above these costs to aid in protecting and administering other wild species that produce no return to the state. It should be remembered that beaver would have disappeared from America in the absence of state control and management and their continued abundance depends upon sound administration by the state.

The trapper's share from beaver ordinarily need not exceed a liberal wage for the time and effort required for trapping and preparing the pelts for market. If he is a non-salaried but bonded trapper who engages in law enforcement activities, his share can appropriately be increased moderately.

Table 4.—APPROXIMATE DISTRIBUTION OF INCOME FROM BEAVER TAKEN UNDER DAMAGE LAWS, 1940–41 (total over $1,000,000).

	Trapped by	
	States	Private individuals
To landowners	$ 1,000	$152,000
To trappers	160,000	453,000
To states	235,000	55,000 (fees)

Whatever the division of income adopted, the game department should have sufficient latitude so that with fluctuation in prices the trapper's share will not become excessively large when prices are high or unprofitably low when prices are depressed. The remainder of the income after shares for the state and trapper have been deducted should go to the landowner.

Some ratios used in dividing the income are as follows:

1. Equal division:
   a. Landowner does trapping and takes 50 per cent; state receives 50 per cent.
   b. State does trapping and takes 50 per cent; landowner receives 50 per cent.
   c. State takes 50 per cent and divides other 50 per cent between landowner and state-selected private trapper.
   d. Landowner takes 50 per cent, state receives 25 per cent state and state-selected private trapper 25 per cent.
2. One-third each to state, landowner, and state-selected trapper.
   a. With a bonded state trapper, the state takes two-thirds, and shares equally with the trapper.
   b. If the trapper is also the landowner, he takes two-thirds, the state one-third.

We believe that the fairest distribution possible would be one-third each to the state, landowner, and trapper.

"HOT" BEAVER PELTS

No other fur animal of comparable value has so wide a distribution and is so easily trapped as the beaver. The intricate network of modern roads and millions of cars which ply them, make it

utterly impossible to prevent illegal traffic in beaver pelts through control of local poaching by game-wardens. All of the eleven western states therefore consider the beaver a special case and require all pelts to be identified by a suitable state stamp or tag. In some a landowner with a trapping permit need merely request such tags, in others a state warden affixes the tags, and in still others the pelts must be sent to the state office to be stamped or tagged. Lack of uniformity between the states and some ineffective requirements leave many loopholes in the system.

Two of the three states which issue permits and tags to landowners, tagged half of all the beaver taken during the 1940–41 season. These two states, however, contain only about one-fourth of the beaver in the west, and the officials, as well as those of adjacent states, feel that a considerable proportion of the beaver which they tagged were "imported."

Another large source of illegal beaver pelts is from Indian reservations. Following a beaver survey of one reservation, one state estimates that it issues each year more tags to Indians than the total beaver population of the reservation. Probably the best solution to this problem would be joint surveys by state departments and representatives of the Indian tribes and the formulation of cooperative agreements that would adjust the number of beaver pelts which may be sold by Indians to the capacity of the reservation in producing them. It is customary for only a few Indians to trap and profit from beaver on the reservations, so that most tribal councils could be persuaded to adopt regulatory measures to benefit a greater number of their members.

Even if these more obvious factors which foster poaching were corrected, there is a large illegal traffic in untagged pelts. Thus one state, using under-cover methods in 1941–42, purchased 465 beaver pelts (besides 19 marten, 6 otter, and 2 racoons) from 13 persons at an average cost of $6.22 per pelt. These were resold by the state through legitimate channels at an average of $13.00 each. Had there been more time before it was necessary to prosecute the cases, the under-cover agent who made these arrests estimated that he could easily have purchased 1200 more pelts. He also estimated that in the entire state almost 5,000 pelts change hands illegally each year.

Both tagged and untagged pelts finally reach the dressers and fur manufacturers where, at present, opportunities for inserting "hot" pelts are unlimited. No really effective method for eliminating illegal traffic with beaver in the United States will be found until these opportunities are eliminated. It is felt that a successful system can be worked out if all states will adopt a uniform procedure for tagging and inspection and the federal government will cooperate with the states under the Lacey Act.

A suitable tagging system would make possible the identification of pelts from the time of skinning to the final cutting. The tag should be small and button-like, resistant to chemicals, should not interfere with dressing processes, and be so constructed that its removal will result in its being destroyed so that it can not again be

used. The problem of producing such a tag has been submitted to E. I. Dupont DeNemours and Company for suggestions.

Another highly important measure used by eight states to lessen the traffic in "hot" beaver is a provision in the laws that restricts the legal sale of beaver pelts to state game authorities. States without such an arrangement afford convenient outlets for pelts from surrounding states. As more states enact stricter laws for the management of their beavers, this matter will become increasingly important in the few states without this requirement.

OTHER DESIRABLE PROVISIONS OF UNIFORM BEAVER LAWS

Several other factors are important in considering policies for the sound administration of beaver. Chief among these is recognition of beaver as a product of the land which requires intensive management if the greatest returns are to be realized. Few landowners can devote sufficient time and study to the problem to equip them with a thorough understanding of the beaver and its environmental requirements. Consequently the state should be responsible for advising landowners on how best to manage beaver for each type of stream. Furthermore, on public lands the states may frequently need to manage beaver themselves.

To make management possible on private lands, a state department should have authority to enter into management agreements with either individuals or groups of landowners, including financial agreements for both the expenditure of funds and the division of income. The state should also have authority to determine the carrying capacity of both private and public streams, to census these streams, and finally to decide with the approval of each landowner the size of a reasonable yearly harvest in accordance with these factors.

The state alone should promulgate trapping regulations. Because of the many advantages that accrue from maintaining a highly expert force of trained trappers, provision for these is advisable, but the regulations should be sufficiently flexible so that the state may vary its system to meet changing conditions. Several states use livetraps exclusively in both pelting and restocking operations. These enable the rejection of kits, pregnant females, and animals with unprime pelts. Oregon has found it highly advantageous to require all trappers to brand their traps and to register their brands with the Game Commission. Unbranded traps may be confiscated.

There is also the important matter of regulations concerning beaver damage. The state department alone should have authority to remove beaver that are damaging private property. Beaver so removed, unless in beaver management units, can advantageously become the

Table 5.—ESTIMATED BEAVER PRODUCTION AND POPULATION IN THE WESTERN STATES.

Pelts taken, 1940–41,	
Under damage laws	45,000
Under management	1,000
Poached	14,000
Potential harvest under sustained yield management	255,000
Present total population	316,000
Potential population of present ranges	550,000

sole property of the state. This will enable the state to maintain suitable "farms" where beaver may be held for a few months to a year or more so that they need not be pelted as kits or when their fur is unprime. Such "farms" could be maintained in places where the migration of beaver to localities on which they could cause damage is unlikely.

Finally, most states possess laws providing for fur farms, and beaver may be included in this field. Some of the more appropriate regulations governing these farms are as follows:

1. All pelts can suitably be sold by the state or their sale should be cleared through the state.

2. A charge might be made by the state for tagging and handling these pelts.

3. Beaver farms should either be fenced to prevent movement on or off of the farm, or be sufficiently isolated from other stocks of beaver so that movement onto the farm is not probable.

4. The operator can be required to pay the state the full value of the original breeding stock and thereafter not required to share the pelt value with the state.

5. Beaver farmers are not allowed to sell live beaver under provisions of existing state laws.

ECONOMIC ASPECTS OF BEAVER ACTIVITIES

Beaver have been building dams and spreading silt-laden, torrential waters across the rock strewn and rugged valleys of America since the Pliocene. Nowhere else in the world have the soil deposits of similar aged valleys grown as deep, as level, or as fertile. Of all continents, ours alone has profited during recent geological times from the activities of beaver and to them we owe the wealth of many of our richest agricultural valleys.

The primeval American scene has changed greatly since the trappers of a century ago virtually cleared the West of beaver. Today the species is multiplying in a highly developed agricultural civilization, but its activities are not all beneficial; the trees cut for food and structures may be valuable orchard trees and the lands flooded may be planted to crops.

Until recently many of us often viewed beaver damage somewhat as an "armchair conservationist" considers overpopulations of deer—something to be expected and borne because we have disturbed nature's "all-wise balance!" With beaver again abundant, this Victorian philosophy must be replaced by a more practical attitude. Henceforth the beaver must be restricted, so far as possible, to lands where any damage done will be more than offset by the combined value of its beneficial activities and its fur.

There are a few areas in the West where beaver cannot now be tolerated such as the fertile delta lands of California where the San Joaquin and Sacramento rivers flow into Suisun Bay. Huge levies there exclude the tide- and river-waters from the tideland farms, and a single colony of the famed Golden Beaver, by breaking a levy, can flood hundreds of acres and produce losses amounting to thousands of dollars.

The most widespread and perennial damage occurs on irrigation projects

which create many news streams in the form of canals and ditches. Arising largely from mountain streams, they provide ideal routes of travel and beaver on arriving at a suitable site for home building immediately set to work to dam these ditches. Removing a dam is useless for the next night it is rebuilt. So long as we have beaver it will be necessary to maintain live-trapping crews constantly engaged in removing beaver from irrigation districts and either transplanting or pelting them as size, pelt, and season dictate. In the same category is the damage to crops and meadows when beaver dam up streams in agricultural areas; removal is the only effective remedy. With orchards and shade or ornamental trees, removal may not always be necessary under intensive beaver management since trees may be protected against cutting by wire mesh screens. Repellants also may serve successfully in these places.

Some cattle are injured or killed by breaking into the bank dens of beaver, and others are lost through the ice when crossing meadow streams which have been dammed so completely by beaver that open, fast-water crossings are lacking. The loss of half a dozen cows each winter from such causes may turn an otherwise friendly rancher into a militant opponent of beaver in his meadows.

Damage outweighs the benefits from beaver activities in intensively farmed localities, but the balance of values is distinctly on the beneficial side through most of the arid West, where the great problem is to procure adequate summer water for livestock and for the irrigation of small and isolated homesteads. Thousands of western streams that arise in the high mountains regularly become torrential soil-eroding floods in the lowlands during the spring run off and then subside to leave dry creek beds during the heat of summer. Since the reestablishment of beaver, many such streams have been altered so fundamentally that their waters rarely attain flood stages in the spring and they have a stabilized flow through the driest summers. Examples of such benefits in both scientific studies and reports of stockmen are legion and need not be elaborated here.

Another benefit from the summer flow of streams, is subirrigation and the consequent great increase in grass production on stream meadows, particularly in places where by repeated dam construction beaver have raised the water table near the surface. The grass remains green, continues to grow, and produces succulent forage during the dry summers when forage elsewhere on the range has become dry and unpalatable.

Beaver activities also exert an important effect on the production of fish. Stabilization of stream flow in arid regions obviously improves the environment for trout. Many streams which contained no fish or only small individuals before the return of the beaver today produce in abundance and the fish attain to large size. Rapid and cold mountain streams are usually improved for fish by beaver dams, which provide still pools where the water warms more rapidly because of greater exposure to the sun. Warm sluggish streams, except when deep pools are created, may be injured by numbers of beaver dams because the water becomes heated to a

point that the oxygen content is insufficient for trout.

Finally, to the beneficial side of the ledger, there may be added an example of a wholly fortuitous character best classified as "engineering." The city of Salmon on the Salmon River in Idaho some years ago planned to construct a dam for diverting water to a hydroelectric plant at a cost of about $20,000. Before the city could proceed, the dam was built at almost precisely the chosen spot by a colony of beaver!

Thus the administration of renewed beaver resources in the West is today complicated by local and regional economics which are entirely unrelated to the value of the beaver as a fur producing species. No other fur or game animal possesses such potentialities for influencing the economic structure of our western civilization. To this extent the beaver presents a challenge and an opportunity to state game commissions. The soundness and adequacy of the administrative practices we adopt to manage the beaver may one day become a yardstick by which the public measures our worth as public administrators.

ACTIVITIES OF THE CHIHUAHUA DEER-MOUSE IN RELATION TO LIGHT INTENSITY[1]

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Small mammals tend to be less active on bright, moonlit nights than on darker nights. This tendency was noted among the desert mammals of southern New Mexico when marked populations were being retrapped over a long period of time. A smaller percentage entered the traps during the full of the moon than upon the darker nights. It was impossible, however, to measure accurately the effects of light intensity on the activity of the wild populations in their natural environment. Temperature and precipitation probably affected their activities and varying degrees of cloudiness altered the brightness of the moonlight and starlight. Consequently, an experiment was later performed to determine the relative activity of captive desert mammals under controlled intensities of light, using the Chihuahua deer-mouse (*Peromyscus maniculatus blandus*) as a representative desert mammal.

It is well known that wild populations of mice of the genus *Peromyscus* are mostly nocturnal in activity. The activity of captive *Peromyscus* also is confined mostly to the hours of darkness as demonstrated by several investigators, notably Johnson (1926), Behney (1936), and Whitaker (1940). Moody (1929) found that deer-mice (*P. m. gracilis*) discriminate visually between lights of different intensities, but I know of no previous attempt to determine the effect of light intensities such as those of moonlight on the nightly activity of *Peromyscus*.

Lee R. Dice, Director of the Laboratory of Vertebrate Genetics, made many helpful suggestions for planning

[1] Contribution from the Laboratory of Vertebrate Genetics, University of Michigan.

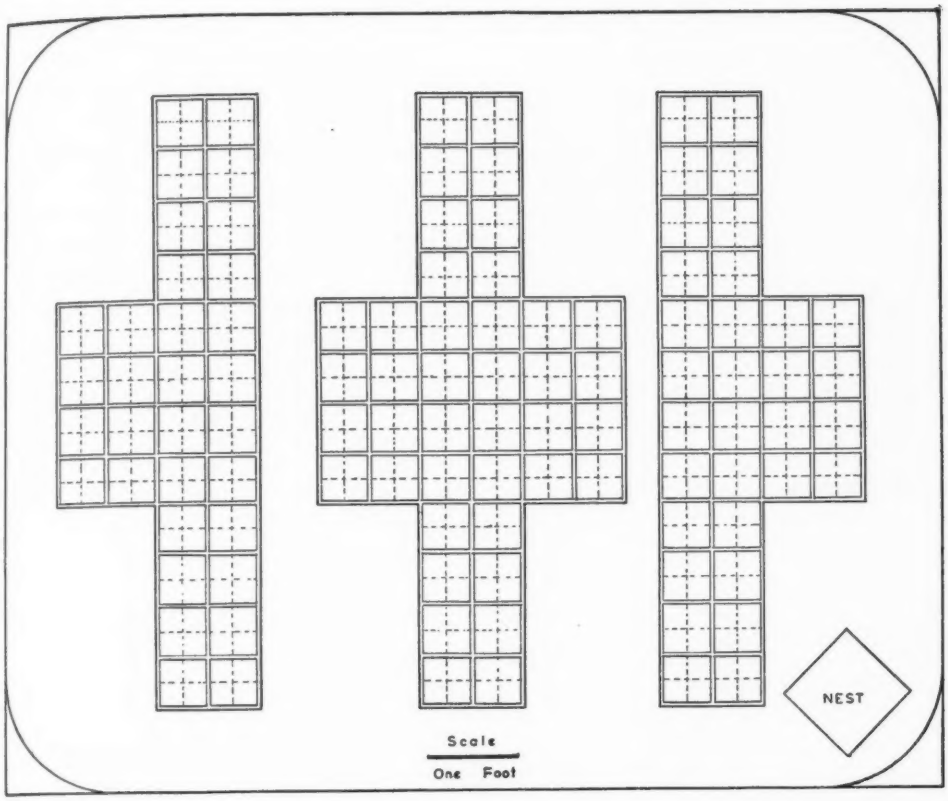

Fig. 1. Diagram of enclosure in which activity of the Chihuahua deer-mouse was studied, showing nest box and location of 3 sets of quadrats that were counted. The reaction room was divided into two such enclosures.

and carrying on this experiment. The statistical calculations are by D. M. Clarke.

METHODS

Experimental area. A light-proofed room was divided by a 24-inch wall into two units, each 10 feet 6 inches by 8 feet 8 inches, and a mouse was placed in a nest box in one corner of each. The nest was provided with food and water so that the mouse did not need to leave the box to obtain them. A thin layer of gray soil was scattered on the floor and smoothed daily with a board. Each mouse was locked in its nest from 8 a.m. until 5 p.m., but during the remainder of the time each was free to leave the nest and run about its respective enclosure.

Each morning quadrats were laid out in a regular pattern on the sand, and the quadrats in which there were no mouse tracks were counted. A movable wooden frame divided into four sections, each 6 inches square, was used to delimit the quadrats. In one part of the experiment, the 6-inch quadrats were subdivided into 3-inch square quadrats by fine wires. The quadrats were laid out every

morning in the same places on the floor. (Fig. 1), so that the scores for any day are directly comparable with those of any other day.

In counting the quadrats, a desk lamp was held so that shadows were thrown in the mouse tracks, to make them conspicuous. All counts were made by myself or by Howard Stroud, a student assistant. Three sets of quadrats were used in each enclosure, one near the nest box, another in the middle of the enclosure, and the third at the opposite end (Fig. 1). In the early part of the experiment, only the 40 quadrats, each 6 inches square, in the middle set were counted; in the last part, both the 6-inch and 3-inch quadrats in all three sets were counted. The near and distant sets each comprised 32 larger and 128 smaller quadrats, the middle set 40 of the larger and 160 of the smaller units

The number of untracked quadrats obviously would vary in inverse proportion to the degree that the mouse moved about during the night; if it did not leave the nest all quadrats would be untracked, whereas if it moved about a great deal, few or none of the quadrats would be untracked

The score for each animal for one night constitutes one mouse-night. Since two mice usually were used simultaneously, one in each enclosure, most nights provided two mouse-night scores.

The Fear Factor. As one important feature of the experimental conditions, a long-eared owl (*Asio wilsonianus*) was caged on the wall of the reaction room. The owl was allowed the freedom of the room during the day but was confined when the mice were free.

The mice used in the experiment were laboratory-reared animals, several generations removed from wild ancestors, frequently handled and relatively tame and unafraid. The owl was kept in the room to create that fear of enemies which affects the activities of wild mice.

After the mice had been in the reaction room a few days they became exceedingly wild. If a nest box was opened the occupant would dash about in a frenzy of fear, very different from the usual reaction of a laboratory mouse, but similar to the behavior of a wild individual. No controls were run without the owl in the room, but the striking change in the behavior of the mice could leave no doubt that they were afraid of the owl. The owl spent much of its time during the day perched on one or the other nest box, and so undoubtedly frightened the mice.

Table 1.—ACTIVITY OF CHIHUAHUA DEER-MOUSE AT SEVERAL LIGHT INTENSITIES.

Mouse nights	Foot candles of light	Mean number of untracked 3-inch quadrats, standard errors, and percentages		
		Near Nest 128 Quadrats	Middle of Room 160 Quadrats	Distant from Nest 128 Quadrats
10	.00082	1.60 ± 2.91 (1.25%)	4.10 ± 2.38 (2.56%)	1.00 ± 0.49 (0.78%)
12	.0012	13.58 ± 5.64 (10.61%)	16.58 ± 8.00 (10.36%)	8.17 ± 4.99 (6.38%)
10	.0070	22.80 ± 8.85 (17.81%)	35.20 ± 8.53 (22.00%)	12.00 ± 3.47 (9.37%)
12	.012	21.17 ± 4.85 (16.54%)	55.00 ± 7.70 (34.37%)	34.58 ± 6.31 (27.02%)
9	.048	96.40 ± 7.05 (75.31%)	89.22 ± 7.87 (55.76%)	51.44 ± 8.07 (40.19%)
10	1.28	128.00 ± 0.00 (100.00%)	160.00 ± 0.00 (100.00%)	128.00 ± 0.00 (100.00%)

After a mouse was placed in the reaction room a conditioning period of 4 nights was allowed before its scores were included in the calculations. The scores during this conditioning period were erratic, and in general the mice were more active at all light intensities than on later nights.

Lights. Over each enclosure and 105 inches above the floor, a white frosted mazda light was centered; at various times bulbs of 50, 25, and 10 watts were used. The light intensity was varied with a 5-step rheostat and with filters of white rag-paper. The wave lengths of light resulting from use of the rheostat or filter papers were not measured.

The amount of light reaching the floor directly under the source was measured by a Weston light-meter (model 603) with a scale reading by .05 foot-candle divisions. Intensities too low for the scale were read at measured short distances below the source, and those at the floor were calculated from such data.

The light intensity in the owl room was changed every 2 to 4 nights during the last part of the experiment, when the data shown in Table 1 were obtained. During the earliest part of the experiment one intensity sometimes was used consecutively for 5 nights.

EFFECT OF LIGHT INTENSITY ON ACTIVITY

The deer-mice showed a clear-cut response to variations in the intensity of light in the reaction room. With no lights, they moved about so freely that each night the entire floor of an enclosure was covered with tracks. As the light intensity was increased the activity decreased until at the higher intensities the mice did not even leave their nest boxes. The average scores (6-inch quadrats) in the middle of the room of 4 male and one female deer-mice 4 to 10 months old were as follows:

Mouse nights	*Foot candles of light*	*Mean number of vacant squares* (Total, 40)
1	no light	0.00
10	.00082	0.20
14	.0012	1.36
2	.0023	0.50
20	.0070	1.20
1	.0090	0.00
12	.012	4.33
3	.018	6.00
12	.048	12.58
15	.061	19.00
7	.14	25.57
1	.26	30.00
2	.40	40.00
10	1.28	40.00
2	1.45	40.00

With no light or a dim light (0.00082 foot-candle), the mice moved about freely, but with 0.40 or more foot-candles of light on the center floor, they were wholly inactive, as all quadrats were untracked.

The scores of 3 males, aged 4 months, on all of the sets of 3-inch quadrats are summarized in Table 1. These show a decrease in activity in all parts of the enclosure as the light intensity was increased. At intensities up to and including 0.012 foot-candle, the mice were more active in both ends of their respective enclosures than in the middle. At .048 foot-candle, there was even less activity at the end near the nest than in the middle, but the mice continued to be more active at the far end than in the middle. The mice then ran along the edge of the wall to the far end and moved about in the latter area. At 1.28 foot-candles, they did not track a single quadrat in any set. Two of the 3 mice never left their boxes under these condi-

tions, whereas the third invariably came out of its nest, made one circuit of the box, then went back into it.

Light intensities that occur in nature are approximated by some of those used in the experiment. Consequently, it is possible to deduce from the experimental data the possible effects of moonlight and starlight on the activity of wild deer-mice. The average illumination by the full moon is a little less than 0.25 meter-candle (W. Carl Rufus, Department of Astronomy, University of Michigan, in letter to Lee R. Dice), equivalent to about .023 foot-candle. Total starlight is approximately one-hundredth that of the full moon, but zodiacal light and auroral luminosity in the earth's atmosphere on the average are of the order of 5 times that of starlight (*idem*). Thus the average illumination from starlight, zodiacal light, and auroral luminosity combined equals approximately .0014 foot-candle.

At .0012 foot-candle, approximately the intensity on a clear, moonless night, the mice were very active (Table 1). At this intensity, they were significantly more active than at .012 foot-candle on both the middle and far sets of quadrats. On the middle set the difference in mean scores was 38.42 ± 11.10 untracked quadrats. The standard errors are large because of the few scores. On the far set the difference was 26.41 ± 8.04 untracked quadrats. It seems probable therefore that, in so far as the effects of light intensity are concerned, wild deer-mice move about freely on clear moonless nights or on nights when there is less illumination.

At .012 foot-candle, about half the intensity of full moonlight, the mice were significantly less active than at an intensity equal to that of a starlit, moonless night, as discussed above. At .048 foot-candle (twice the intensity of full moonlight) the mice were significantly less active than at .012 foot-candle on the middle and near sets of quadrats. On the middle set the difference in means was 34.22 ± 11.01 untracked quadrats. On the near set the difference was 75.23 ± 8.56 untracked quadrats. These data indicate that even a half-moon probably reduces the amount of activity of wild mice, and as the light increases beyond this, the activity of the mice correspondingly decreases.

DISCUSSION

The activity of the deer-mice decreases as the light intensity is increased probably because of fear. Presumably they are aware of increased danger to themselves when their environment is well illuminated, and react by moving about less than on dark nights. In nature, the deer-mice probably range over a smaller area on bright moonlit nights than on darker ones. In the mesquite association of New Mexico it seems likely that the Chihuahua deer-mice seldom leave the clumps of mesquite where their respective nests are located on nights when the moon is full and the sky is clear.

This decreased activity at light intensities equivalent to those of moonlight renders the deer-mice no more, and possibly less, subject to attack by predators during the full, than during the dark, of the moon. They are more visible when the moon is full, but by moving about less they expose themselves less to attack.

These conclusions have a practical application to the censusing of mam-

malian populations. When the moon is full, a smaller percentage of the population undoubtedly will be caught by traps than on cloudy nights or when the moon is dark. This and other factors of the environment affecting the activity of small mammals, make it necessary that trapping to determine population size be continued for a long enough period to capture the whole population. The season of the moon, the air temperature and humidity, and the amount and kind of precipitation may produce variations in the time necessary to catch all of a population. A three-day trap period to census small mammal populations, as advocated by Bole (1939: 57) is therefore probably much too short under most field conditions. Trapping with killer traps, as done by Bole, induces invasion from other areas because of the lowered population pressure, so this type of trapping cannot be continued beyond 3 days at the most without accumulating a large error. Consequently, it is only by the use of live traps and the marking and releasing of captured animals that the size of a resident population can be learned with accuracy. Live-trapping can be continued long enough to capture all residents without introducing a large error by the capture of invading non-residents.

Light intensity probably affects the nightly activity of other species of mammals, as kangaroo rats (*Dipodomys ordii* and *Dipodomys merriami*) and a pocket mouse (*Perognathus penicillatus*) were caught in smaller numbers on moonlit nights in the mesquite association of southern New Mexico than on dark nights. Burt (1940: 25) had the general impression that more wood-mice (*Peromyscus leucopus noveboracensis*) were caught on dark, rainy nights than on clear, moonlit nights.

SUMMARY

The activity of captive Chihuahua deer-mice was tested at light intensities varying from zero to 1.45 foot-candles, and found to decrease progressively as the light intensity was increased. They were very active at an intensity approximating that of a clear, moonless night. Their activity decreased significantly when it was increased to an equivalent of one-half of full moonlight, and it decreased further with greater light intensity. Fear of an owl kept in the reaction room is believed to be partly responsible for the reduction in activity as the light intensity was increased.

LITERATURE CITED

BEHNEY, W. H. 1936. Nocturnal explorations of the forest deer-mouse. Journ. Mammalogy, **17**: 225–230, 4 figs.

BOLE, B. P., JR. 1939. The quadrat method of studying small mammal populations. Cleveland Mus. Nat. Hist. Sci. Publ., **5**: 15–77, 3 figs.

BURT, W. H. 1940. Territorial behavior and populations of some small mammals in southern Michigan. Univ. Mich. Mus. Zool. Misc. Publ., **25**: 1–58, 2 pls., 8 figs.

JOHNSON, M. S. 1926. Activities and distribution of certain wild mice in relation to biotic communities. Journ. Mammalogy, **7**: 245–277, 8 figs.

MOODY, P. A. 1929. Brightness vision in the deer-mouse, Peromyscus maniculatus gracilis. Journ. Exp. Zool., **52**: 367–405, 6 figs.

WHITAKER, W. L. 1940. Some effects of artificial illumination on reproduction in the white-footed mouse, Peromyscus leucopus noveboracensis. Journ. Exp. Zool., **83**: 33–60, 4 figs.

FOOD HABITS OF THE BANNER-TAILED KANGAROO RAT IN ARIZONA

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To supplement an earlier life history study (Monson and Kessler, 1940) of the banner-tailed kangaroo rat (*Dipodomys s. spectabilis*), 65 dens were excavated and their food storages measured and analyzed, from June, 1939,to July, 1940. The study was made in the southern part of the Sulphur Springs Valley, Cochise County, Arizona in an area delimited on the south by the town of Douglas, on the east by the Pedrogosa and Swisshelm mountains, on the north by a line due east from the town of Pearce, and on the west by the towns of Courtland, Gleeson, and Lowell. The elevation is 4,000 to 4,500 feet, and the average annual rainfall about 12 inches. The general vegetation is a mixed browse-grass type, with extensive, almost pure, stands of tobosa grass (*Hilaria mutica*) and sacaton grass (*Sporobolus wrightii*). Mesquite (*Prosopis chilensis* var. *glandulosa*), mescat acacia (*Acacia constricta*), long-flowered catclaw (*A. greggii*), and creosotebush (*Larrea divaricata*) are the browse plants, and Rothrock grama (*Bouteloua rothrockii*), fluffgrass (*Triodia pulchella*), and the three-awns (*Aristida* spp.) are the grasses. In this type, bannertails are most common in a particular association (usually moderately to heavily grazed) of Rothrock grama, mesquite, soaptree yucca (*Yucca elata*), with a variety of less common perennial species and some annuals. Annual vegetation is only locally predominant, and light winter precipitation in 1939–1940 further tended to minimize its role in the storing activities of the banner-tail.

The methods used were essentially those of the previous study. Stored food was removed and measured by volume as excavation proceeded. The material was usually segregated according to species; otherwise, the percentages by species were estimated. Measurement was by volume rather than weight because fine soil particles (and sometimes absorbed moisture) would have disturbed the accuracy of weight measurements of the relatively light stored material. Care was taken to compress the stores uniformly to about the same extent as in the dens. Only fresh material was recorded, that placed in the den within twelve months of the time of excavation.

The 65 dens were excavated by months as follows: 1939–July, 8; August, 7; September, 5; October, 11; November, 8; December, 7. 1940–March 5; May, 7; and June, 7. Since storing activity is slight during the winter, the lack of excavations in January and February does not detract essentially from the record. The lack of excavations in April is partly offset by those in the last few days of March and the first few days of May.

All plant identifications were made by the author with the assistance of Prof. J. J. Thornber, University of Arizona. Dr. Charles T. Vorhies and Robert A. Flock, University of Arizona, helped in identifying the animals; A. E.

Table 1.—FOOD STORES IN 63 DENS OF BANNER-TAIL KANGAROO RAT (**perennial*).

Plants	*No. units*	*Per cent*	*No. quarts*	*Per cent*
Rothrock grama (*Bouteloua rothrockii*)*	1,195	19.9	311.1	26.0
Fluffgrass (*Triodia pulchella*)*	257	4.1	130.2	10.9
Sixweeks three-awn (*Aristida adscensionis*)	430	6.8	127.4	10.7
Aplopappus gracilis	320	5.1	100.2	8.4
*Brayulinea densa**	226	3.6	75.4	6.3
Purple three-awn (*Aristida purpurea*)*	299	4.7	61.6	5.2
Carpetweed (*Mollugo cerviana*)	197	3.1	36.7	3.1
Needle grama (*Bouteloua aristidoides*)	108	1.7	28.0	2.3
Mesquite (*Prosopis chilensis* var. *glandulosa*)*	248	3.9	24.7	2.1
Partridge pea (*Cassia leptadenia*)	149	2.4	22.5	1.9
Sixweeks grama (*Bouteloua barbata*)	46	.7	21.4	1.8
Fiddleneck (*Phacelia crenulata*)	68	1.1	21.0	1.8
Astragalus nuttallianus	133	2.1	20.6	1.7
*Baileya multiradiata**	79	1.2	20.0	1.7
Sorrel eriogonum (*Eriogonum polycladon*)	59	.9	17.6	1.5
Peppergrass (*Lepidium thurberi*)	469	7.4	17.0	1.4
Eragrostis arida	138	2.2	15.8	1.3
Havard three-awn (*Aristida barbata*)*	163	2.6	12.3	1.0
Sacaton (*Sporobolus wrightii*)*	111	1.8	12.0	1.0
Trompillo (*Solanum elaeagnifolium*)*	126	2.0	11.8	1.0
Foothill deervetch (*Lotus humistratus*)	225	3.6	9.6	.8
Tumbleweed (*Amaranthus graecizans*)	46	.7	8.8	.7
*Bahia absinthifolia**	26	.4	8.1	.7
Arizona panicum (*Panicum arizonicum*)	29	.5	6.9	.6
Poverty three-awn (*Aristida divaricata*)*	141	2.2	6.5	.5
Desert zinnia (*Zinnia pumila*)*	36	.6	4.9	.4
*Evolvulus sericeus**	45	.7	4.7	.4
Spike pappusgrass (*Pappophorum wrightii*)*	35	.6	4.7	.4
Cocklebur (*Xanthium commune*)	70	1.1	4.5	.4
Stinkgrass (*Eragrostis cilianensis*)	35	.6	4.5	.4
Vine-mesquite (*Panicum obtusum*)*	51	.8	4.5	.4
Desert Indian-wheat (*Plantago ignota*)	92	1.5	4.3	.4
Mormon tea (*Ephedra nevadensis*)*	41	.6	2.5	.2
Mescat acacia (*Acacia constricta*)*	2	tr	2.1	.2
Burroweed (*Aplopappus tenuisecta*)*	7	.1	1.8	.1
Burrograss (*Scleropogon brevifolius*)*	53	.8	1.5	.1
Spider grass (*Aristida ternipes*)*	135	2.1	1.5	.1
Bladderpod (*Lesquerella gordoni*)	29	.5	1.4	.1
Feather fingergrass (*Chloris virgata*)	5	.1	1.0	.1
Pectocarya gracilis	2	tr	.8	.1
Unicorn plant (*Martynia altheaefolia*)*	4	.1	.7	.1
Tobosa grass (*Hilaria mutica*)*	150	2.4	.7	.1
Arizona cottongrass (*Trichachne californica*)*	4	.1	.6	tr
Senna (*Cassia bauhinioides*)*	1	tr	.5	tr
*Astragalus lentiginosus**	23	.4	.5	tr
Mentzelia asperula	5	.1	.5	tr
New Mexican feathergrass (*Stipa neomexicana*)*	1	tr	.4	tr
*Acacia suffrutescens**	2	tr	.4	tr
*Oenothera mollissimus**	1	tr	.4	tr
*Hoffmanseggia jamesii**	16	.2	.4	tr
Soaptree yucca (*Yucca elata*)*	5	.1	.3	tr
*Hoffmanseggia drepanocarpa**	13	.2	.2	tr
*Jatropha macrorhiza**	1	tr	.1	tr
*Allionia incarnata**	2	tr	.1	tr
*Chamaesaracha conioides**	1	tr	.1	tr
*Aster tanacetifolius**	20	.3	.1	tr
Malacothrix fendleri	2	tr	.1	tr
Wright's buckwheat-brush (*Eriogonum wrightii*)*	30	.5	tr	tr
Plains bristlegrass (*Setaria macrostachya*)*	2	tr	tr	tr
Taparosa (*Anisacanthus thurberi*)*	2	tr	tr	tr
Ground pearls	30	.5	1.7	.1
Miscellaneous	59	.9	14.1	1.2
Totals	6,300		1,193.9	

Borell and Lawrence V. Compton, Soil Conservation Service, gave assistance in preparing the manuscript.

Table 1 presents the statistics on food storage: (1) By units, considering the total storage of each den to be 100 units, regardless of the actual volume stored; and (2) by volume in dry quarts. Two dens holding no storage were disregarded. "Ground pearls" are small clusters formed by scale insects (*Margarodes*) on plant roots. "Miscellaneous" includes traces of plants too small for measurement. The stored plant material was mostly seeds, seed heads, or seed vessels, but occasionally leaves, flowers, or cut stems. Pieces of horse and cattle dung were frequent in the storage caches, but are not considered part of the food.

Table 2.—SUMMARY BY CLASSES OF PLANT MATERIAL STORED (*percentages*).

	Present study		*Previous study*[b]
	units[a]	*volume*	*units*[a]
Annual grasses	12.5	17.2	59.7
Perennial grasses	41.2	45.9	13.4
Annual non-grasses	29.6	22.2	15.2
Perennial non-grasses	15.2	13.4	8.2
Total annuals	42.2	39.4	74.9
Total perennials	56.4	59.3	21.6
Total grasses	53.8	63.0	73.1
Total non-grasses	44.8	35.6	23.3
Totals	98.6	98.7	96.5

[a] On the basis of analysis by 100 units storage per den (excluding amounts not large enough to be reckoned), in addition to ground pearls and undetermined material.
[b] Monson and Kessler (1940).

Table 2 summarizes the material in the present and the previous study as to whether the plants were annual or perennial and grasses or non-grasses. Perennial grasses are regarded as most essential and annual non-grasses as least important to livestock grazing. An appraisal of the food habits of the banner-tailed kangaroo rat as they affect grazing may be made from these data. These statistics are not claimed to represent exact averages because of the extremely small percentage of all dens excavated in the study area, and because yearly climatic variations may affect markedly the available plant food. The amount of food eaten but never stored, especially green food, may reach considerable proportions at some seasons and should be considered.

The amount stored per den is recorded in Table 3 and the average storage by months in Figure 1. The results of this series of excavations as compared with the previous study (Table 2), show

Table 3.—AMOUNTS OF FOOD STORED IN EACH OF 65 DENS.

Date	*Quarts*	*Date*	*Quarts*
July 6	3.8	Nov. 3	54.0
July 7	5.6	Nov. 8	43.8
July 11	6.2	Nov. 8	18.0
July 17	11.7	Nov. 9	37.2
July 21	4.0	Nov. 13	75.0
July 21	0.1	Nov. 15	55.6
July 24	6.4	Dec. 11	38.5
July 31	0.8	Dec. 12	37.0
Aug. 1	12.4	Dec. 12	37.8
Aug. 2	1.0	Dec. 13	20.2
Aug. 4	26.4	Dec. 13	30.7
Aug. 7	10.4	Dec. 14	21.0
Aug. 8	7.3	Dec. 14	26.8
Aug. 8	None	Mar. 26	11.7
Aug. 9	1.5	Mar. 27	0.4
Sept. 15	11.8	Mar. 28	4.0
Sept. 27	10.4	Mar. 28	1.2
Sept. 27	10.3	Mar. 29	1.6
Sept. 28	1.0	May 1	3.3
Sept. 28	0.3	May 2	6.0
Oct. 4	9.5	May 2	0.7
Oct. 4	18.7	May 3	2.2
Oct. 12	21.8	May 3	0.1
Oct. 16	22.3	May 15	3.4
Oct. 16	0.5	May 15	0.1
Oct. 18	107.0	June 3	40.2
Oct. 20	11.0	June 4	2.0
Oct. 23	21.2	June 4	3.5
Oct. 23	51.5	June 5	1.2
Oct. 25	41.0	June 5	None
Oct. 25	53.7	June 11	4.6
Nov. 2	70.4	June 13	0.6
Nov. 2	51.5		

differences, largest for the perennial grasses and smallest for the total grasses. These probably result from availability; in the previous study area, principally the San Simon Valley of Arizona, annual gramas were the predominant plants bearing seeds, and in the present study area Rothrock grama (a short-lived perennial) was most abundant. Rothrock grama is uncommon in the San Simon Valley. Of non-grasses there is a difference of 11.5 per cent, accounted for by much *Haplopappus gracilis*, *Brayulinea densa*, and carpetweed in the present investigation, and the small amounts of non-grasses in the earlier study. These three plants are common in the Sulphur Springs Valley, but not in the San Simon Valley. The general conclusion, therefore, is that banner-tails are prone to gather those seeds that are most available in their individual ranges. Such seeds in both areas are largely those of annual grasses (except Rothrock grama) and non-grasses—plants that bear prolific seed crops. The more valuable perennial grasses generally do not seed freely. Availability rather than palatability appears to be the governing factor in choice of material for storing.

This study, as well as the previous one, shows that banner-tails are not found common in country dominated by perennial grasses, which do not provide an abundant and unfailing crop of seeds as do the annual grasses and weeds.

MISCELLANEOUS DATA

The average surface mound was 8 by 8 feet, its average maximum height 15.6 inches, and the average of the deepest point in the burrows 25.3 inches. One or more banner-tailed kangaroo rats were found in 53 of the 65 dens excavated. Only one was found in each of 41 burrows; in the others, the occupants were as follows: adult female

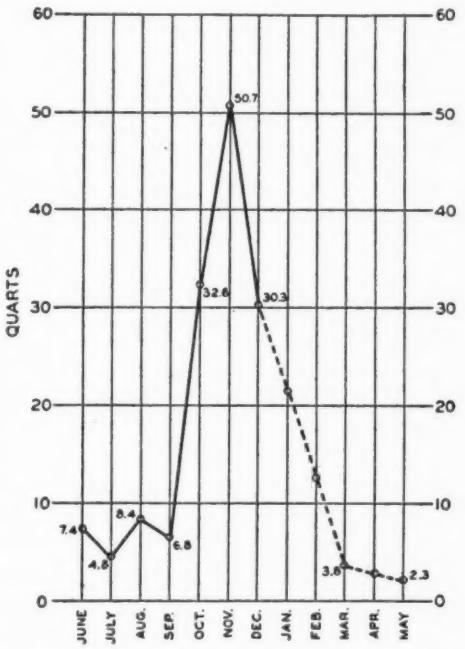

Fig. 1. Monthly den storage of the Banner-tailed Kangaroo Rat. No dens excavated in January, February, or April.

with two young, 3 dens; adult (sex ?) and two young, 1 den; adult female and one young, 3 dens; two young, 1 den; two adult females and one young, 1 den; adult male, adult female, and one young, 1 den; adult female and adult (sex ?), 1 den; and two adults (sex ?), 1 den. A den excavated on December 14 held an adult female and a half-grown young (included in the above) on a date beyond the usual breeding season (Vorhies and Taylor, 1922, p. 17).

Commensals common in the dens were: cave crickets (*Ceuthopilus lamel-*

lipes), cockroaches (*Arenevaga erratica*), scorpions (*Centrurus sp.* and *Vejovis sinigerus*), black widow spiders (*Latrodectus mactans*), centipedes, and various other insects and spiders. Whip-tail lizards (*Cnemidophorus* sp.) also were present frequently. A toad was found at the bottom of one of the deeper dens, a cottontail rabbit (*Sylvilagus auduboni*) in one, rattlesnakes (*Crotalus* sp.) in two, a gopher snake (*Pituophis* sp.) in one, and a king snake (*Lampropeltis getulus*) in one.

SUMMARY

To investigate further the food habits of the banner-tailed kangaroo rat, 65 dens were excavated and the food stores in them analyzed during 1939 and 1940 in the Sulphur Springs Valley, Arizona. Seeds and other parts of more than 80 species of plants were found. There were represented more grasses than non-grasses, and consisted chiefly of Rothrock grama (a short-lived perennial) and various annual grasses. The remainder of the cached food comprised annual weeds and small perennials.

LITERATURE CITED

MONSON, GALE, AND WAYNE KESSLER. 1940. Life History Notes on the Banner-tailed Kangaroo Rat, Merriam's Kangaroo Rat, and the White-throated Wood Rat in Arizona and New Mexico. Journ. Wildl. Mgt., **4**: 37–43.

VORHIES, CHARLES T., AND WALTER P. TAYLOR. 1922. Life History of the Kangaroo Rat, *Dipodomys spectabilis spectabilis* Merriam. U. S. Dept. Agric. Bul. **1091**: also Univ. Ariz. Agric. Exp. Sta., Tech. Bul. **1**.

MANAGEMENT STUDIES OF THE COTTONTAIL RABBIT IN SOUTHWESTERN MICHIGAN[1]

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The annual kill of cottontails (*Sylvilagus floridanus mearnsii*) by licensed hunters in Michigan is over 2,000,000 individuals. Little effort heretofore has been made to determine habitat requirements and develop management measures for this species, the two most extensive previous studies being those of Trippensee (1934) and Allen (1938).

The present study was initiated in January, 1938, to evaluate effects of various management procedures. These included construction of brush piles and

[1] From a thesis for the Ph.D. in the University of Michigan.

The Michigan Department of Conservation provided a part-time fellowship and other support for this study. H. D. Ruhl, Chief of the Game Division, gave encouragement and advice. Lee R. Dice directed the studies and preparation of the thesis. W. H. Burt gave many helpful suggestions. D. L. Allen, then Biologist in charge at the Swan Creek Station, contributed field records and supervision. U. S. Department of Agriculture and Works Progress Administration constructed brush piles and did other developmental work on the study area, F. J. Hodge being in charge. Betty M. Robertson identified the plants; field records were contributed by F. W. Stuewer and P. S. Baumgras.

artificial burrows, artificial stocking and distribution of artificial food during winter. In addition to studying populations in the various areas managed, the investigation included most phases of the life history of the rabbit.

The vicinity of the Swan Creek Wildlife Experiment Station near Allegan, Michigan, was chosen as the location for the studies because of the facilities available and the presence of a large acreage of sub-marginal land. The State of Michigan owns a considerable amount of such land with little value for agriculture. It has, therefore, been the aim of this investigation to find some practical means of increasing rabbit populations on such poor lands, and to make them more useful as public hunting grounds.

AREA STUDIED

The study was conducted chiefly in Valley Township (T2N, R14W, Secs. 5, 8), and Heath Township (T3N, R14W, Secs. 31, 32). The soil is Plainfield Sand ("Allegan Sand," Fippin and Rice, 1901) 30 to 60 feet in depth, with but little organic matter in the surface layer. The land is generally of third class, submarginal, or locally marginal (Veatch, 1933).

The topography is generally flat with the Kalamazoo River and its extensive bayous cutting through a wide meandering valley. Abrupt escarpments rise 50 to 60 feet and separate the sandy upland from the fertile river-bottom.

Climate. The annual precipitation is about 30 inches, including 60 inches of snowfall (Fippin and Rice, 1901). The mean annual temperature is about 48°F., the average annual maximum 95.5°F., the average annual minimum, −12.1°F., and the average crop growing season is about 160 days (Leverett, 1917). Weather during 1938 and 1939 was not unusual.

History. Extensive forests were present in Allegan County when white men first settled there in 1831. The sandy plains immediately west of the city of Allegan then had extensive sparse growths of small "buckwheat pine" (Fippin and Rice, 1901). Most of this timber had been removed by 1870, and a shrubby growth of oak, sassafras, and poplar soon sprang up among the remaining pine. Some interspersion of beech, maple, and oak occurred along the borders of the pine forests. The heavier soils and lowlands in the county were originally covered densely with hardwoods. Cultivation was attempted after the pine forests were cleared, but the settlers, who usually owned 40 to 80 acres, could not make a living from the unproductive soil. In 1935, the U. S. Department of Agriculture began purchasing the submarginal lands in this area in the resettlement program and set it aside for conservation and recreation purposes.

Vegetation.—The trees on the sandy uplands are mainly oaks (*Quercus alba* and *Q. velutina*) up to about 10 inches in average diameter at breast height, with some sassafras, cherry, and dogwood. The deserted farm lands are slowly being invaded by weeds, dewberry, sassafras, cherry, and oaks. Local patches of "blow sand" have been partially stabilized by soil conservation measures. The composition of the present day vegetation is little different from that of 50 years ago, according to old settlers.

Individual study areas. Five 160-acre

upland experimental areas, here termed "quadrats," were selected in 1938, and designated according to the management measure applied; the fifth was held as a check area.

ARTIFICIAL BURROW AREA. The eastern two-thirds supports a dense stand of second-growth oak (white and black) 4 to 8 inches in diameter, and because of a general lack of shrubs is not well suited for rabbits. The cover on the remainder is favorable to rabbits, ranging from scattered oaks 3 to 6 inches in diameter to intermittent clumps of reproductive growth. Some New Jersey tea (*Ceanothus americanus*), wormwood (*Artemisia caudata*), and black cherry (*Prunus serotina*) is present.

STOCKING AREA. The main cover is of white and black oaks up to 3 inches (D.B.H.) and a few from 6 to 9 inches in diameter; the forest canopy is open. About 7 acres, once cultivated, are now covered with wormwood and grasses. Jersey tea is more abundant than on any of the other quadrats. The area contains more good rabbit cover than the other plots.

ARTIFICIAL FOOD AREA. This has a scattered stand of 4- to 8-inch oaks interspersed with moderate oak reproduction. About 15 acres, once cultivated, now support wormwood (Pl. 5, *A*) and scattered clumps of oak reproduction. The cover is comparable to that on the Stocking Area and on the western third of the Artificial Burrow Area.

BRUSH-PILE AREA. A dense stand of oak 5 to 10 inches in diameter covers 145 acres, the remainder being abandoned farm land with a dense growth of wormwood, a moderate amount of sassafras (*Sassafras albidum*), and a little flowering dogwood (*Cornus florida*) predominating in the ground cover. The trees are larger and the forest canopy is denser than on the other study areas.

CHECK AREA. Oaks 5 to 10 inches in diameter cover the entire area which differs from the other study plots in not including any abandoned fields. Approximately half of it has almost no ground cover, but the remainder supports some small oak reproduction.

Hollow Trees and Burrows on Upland. A few oak trees (about 1 per 20 acres) have small hollows in their bases and such holes are often used by rabbits (Pl. 5, *E*). Hollow pine logs are often frequented, but their scarcity (about 1 per 40 acres) limits their value. Woodchucks and skunks are seldom found on the upland, and, accordingly, their burrows are usually lacking. One or more badgers living in the vicinity were not known to use more than three or four burrows. Evidently, the scarcity of ground squirrels provided little opportunity for badgers to dig in pursuit of such prey. A few upland sites lack suitable winter cover (burrows, brush piles, coppice); consequently, the rabbits migrate to the bottomlands during that season.

Food. The foods most available on the upland during winter were taken most frequently. The bark, twigs, and buds of white oak, flowering dogwood, sassafras, and Jersey tea were taken in liberal amounts (Haugen, 1942b).

METHOD OF STUDY

Information about the cottontail has been secured by live-trapping, shooting, necropsy, examination of burrows, tracking, scatology, and field observation.

Trapping technique. Forty-nine permanently numbered trap stations were established on each quadrat in a grid at 110-yard intervals; the outside rows of traps was 110 yards inside the quadrat boundaries. With this permanent spacing, the size of the area effectively trapped changes somewhat with change in the average size of the home range of animals living along the borders. During summer most of the rabbits taken are young with an average range of 9.3 acres (Haugen, 1942a) so that the entire quadrat of 160 acres will be effectively trapped. The average home range of the population increases above 10 acres (a cruising radius of about 110 yards) during fall, winter, and early spring, and then the area effectively trapped was slightly larger than the 160-acre study plots.

Live-traps (Pl. 5, *C*) were set near the most suitable cover within 50 feet of the "station," usually with the opening toward the base of a clump of bushes or a tree. A combination of ear-corn, rolled oats and apple bait was used, and the traps were visited each morning. The rabbits taken were closely examined for ectoparasites and breeding condition, and a series of measurements was recorded (Haugen, 1942b). When each was first captured it was marked with a numbered "fingerling" or butt-type ear-tag. Tag numbers of rabbits previously marked were recorded with other data noted.

Reliability of census methods. One of the most difficult problems in game management is that of checking population density. Investigators have met this difficulty with a variety of methods, most of them extensive in nature. Estimates of populations have been obtained by direct observation, fecal pellet count, tracking, shooting, and trapping. Tracking, pellet counts, and direct observation give an index to the population, but the results are often limited in application and difficult to interpret. Tracking is limited to seasons of snow, or to local dusty areas. Shooting obviously is disadvantageous in that the population is sacrificed, thereby preventing a recount.

Live-trapping and marking requires considerable labor and expense, but if properly done gives a reliable index to the number of rabbits present. The size of quadrat, type and location of traps, bait, weather, dispersal, migration, individual (rabbit) behavior, and the length of the trapping period all influence the number of rabbits caught.

The size of the quadrat to be censused has an important relationship to the results obtained. Bole (1939) found that as the size of a quadrat was increased, the apparent population density of small mammals decreased. The chance for drifting animals to move across an area and be counted is proportionately reduced as the size of the quadrat increases (Dice, 1938) because the area increases at a greater rate than the perimeter. The relationship between size of area censused and size of home range of the species studied is particularly important. The area censused obviously should be at least several times that of the average home range. The quadrats in this study were about 7 times the average home range of an adult female cottontail (Haugen, 1942a) and consequently considered adequate for population study. The type of traps employed, their spacing, and the bait technique were standardized, and are

believed to have been equally efficient at all times.

Five juvenile males, 16 adult females, and 26 adult males reappeared in the traps after an absence of one or more

method does not sacrifice individuals and population density can be rechecked from time to time. It also allows a simultaneous study of the life history and populations.

Table 1.—AVERAGE DISTRIBUTION OF "NEW" CAPTURES AND RECAPTURES OF INDIVIDUAL COTTONTAILS ON SIX STUDY AREAS, AS TO THE RELATIVE POSITION OF DAY WITHIN TRAPPING PERIOD; 1938–1939.

Day in trapping period	Number of trapping periods	For each day of trapping period				
		Total new captures	Average of new individuals	Total recaptures	Average of recaptures	Total catch
1	46	131	2.85 (*100%*)	0	0.0	131
2	46	79	1.72 (*84%*)	15	.3	94
3	46	67	1.46 (*61%*)	43	.9	110
4	46	58	1.26 (*56%*)	46	1.0	104
5	46	45	.98 (*47%*)	50	1.1	95
6	45	48	1.07 (*35%*)	88	2.0	136
7	44	34	.77 (*31%*)	75	1.7	109
8	43	33	.77 (*29%*)	79	1.8	112
9	43	29	.67 (*25%*)	88	2.0	117
10	42	30	.71 (*29%*)	73	1.7	103
11	38	25	.66 (*24%*)	78	2.1	103
12	35	20	.57 (*19%*)	88	2.5	108
13	33	11	.33 (*14%*)	69	2.1	80
14	31	19	.61 (*25%*)	57	1.8	76
15	24	6	.25 (*13%*)	39	1.6	45
16	22	8	.36 (*15%*)	45	2.0	53
17	20	10	.50 (*18%*)	45	2.2	55
18	16	4	.25 (*12%*)	30	1.9	34
19	12	10	.83 (*32%*)	21	1.7	31
20	6	1	.17 (*11%*)	8	1.3	9
21	5	4	.80 (*18%*)	18	3.6	22
22	5	4	.80 (*18%*)	19	3.8	23
23	5	2	.40 (*25%*)	6	1.2	8
24	4	3	.75 (*17%*)	15	3.7	18
25	4	1	.25 (*14%*)	6	1.5	7

immediately previous census periods. Chances for reappearance decreased as the length of the absence increased. Some of these animals may have temporarily shifted their ranges.

Live-trapping has several advantages over other census methods. The recapture of ear-marked individuals frequently gives evidence as to whether they are resident or transient. The

Duration of trapping necessary to capture all individuals. A steady decline in capture of new rabbits (those first handled during any given census period) occurred from the first to the fifth day of a census period (Table 1; Fig. 1). The diminishing yield of new individuals was especially rapid during the breeding season and fall, but less so during winter. From the 6th to the 10th

days of a trapping period, the decline was small. After the 10th day, the daily catch of additional individuals continued at an average rate of about one new rabbit per 2 days of trapping. Probably these were mainly non-residents (drifters) which were taken in fluctuating numbers.

During winter, daily catches of new individuals were distributed rather evenly over the first 9 days of a census. After the 9th day in winter trapping, the percentage catch of new individuals decreased sharply and few new individuals were taken after the 10th day. Evidently, rabbits have more securely established ranges in this season.

The trend of the diminishing daily yield of new individuals (Fig. 1) is similar to that found by Bole (1939) and Burt (1940) for smaller mammals. Their skew curves (rapidly decreasing yield of individuals) declined sharply from the first to the third days of trapping, then continued at a low but fairly constant level.

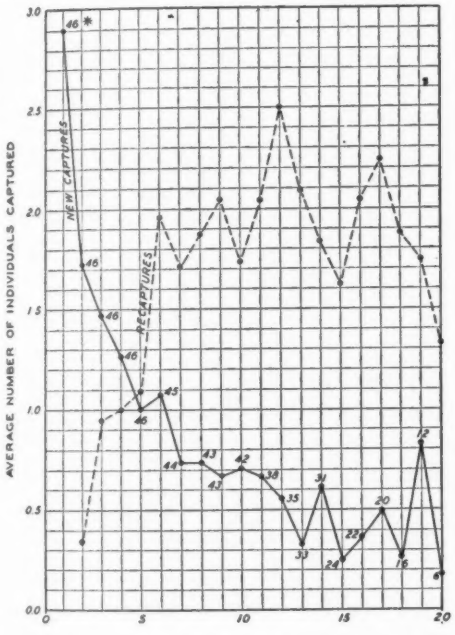

Fig. 1. Average daily catch of cottontails per 160-acre quadrat for first 20 days of trapping based on records from six quadrats; *number of trapping periods on which average is based.

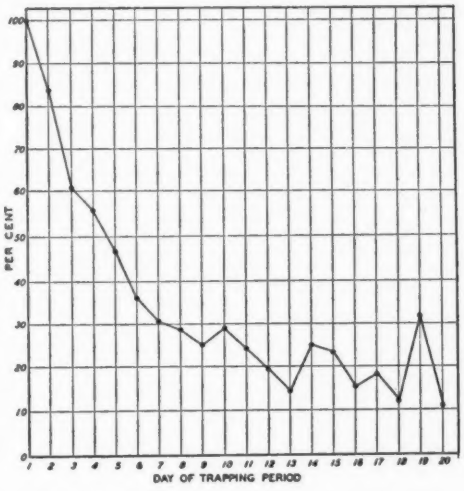

Fig. 2. Percentage of new individuals among the total catch of cottontails for any given day of a trapping period (all ages and both sexes combined).

Under the conditions of the present study ten days of live-trapping apparently were sufficient to census an area; consequently, all population figures given here are based on ten days of live-trapping. A census by this method will not be entirely accurate, but censuses on different areas of generally similar size, or on the same area at different times should be comparable. Due to the geometric spacing (grid pattern) of traps, more time was required to census the areas than if the traps had been more strategically placed.

Non-resident rabbits. Rabbits without established ranges on an area, but which

moved on across or off an area were termed "drifters." The majority of new individuals taken after the 10th day of trapping during the breeding season and fall period were probably drifters (Fig. 2), although a few may have been residents which had escaped previous capture. A few non-residents may also be taken during the first 10 days of trapping, but there is no known method which will determine the exact proportion of the population which these individuals represent.

EFFECTIVENESS OF MANAGEMENT PRACTICES

Each study area was censused by live-trapping once each 3 months during 1938 and 1939.

CHECK AREA

Apparently only six rabbits (2 female, 4 males) occupied this area at the original census in late February, 1938. Three months later (June 17–July 2) only seven (1 juvenile male, 2 female and 4 male adults) were taken. It is not surprising that the population had not increased appreciably because at each census only 2 adult females were found, both occupying ranges partly outside the area.

By the fall of 1938, the population had increased to 12 (juveniles: 3 females, 2 males; adults: 3 females, 4 males). Of the adults, one female and one male captured may possibly have been physically mature young of the year.

The late winter (February, 1939) population was five (2 females and 3 males). At least three of them occupied "borderline ranges" along the margins; one female and a male ranged into a leather-leaf bog which provided the best cover available either in or adjacent to the area.

During May, 1939, 16 were secured (juveniles: 2 females, 2 males; adults: 5 females, 7 males). Cottontails were then more numerous on this area than at any other season during 1938 or 1939.

A July, 1939, census accounted for only 7 rabbits (juveniles: 3 females, 1 male; adults: 2 females, 1 male), less than half those present in May. Six adult males and 3 adult females present in May were not retaken at this time. A marsh hawk nesting in the nearby leather-leaf bog perhaps was partly responsible for the apparent decline in numbers. Hind feet of juvenile rabbits were frequently found at the hawk's nest.

During October, 1939, 9 rabbits were counted (juveniles: 1 female, 5 males; adults: 2 females, 1 male). The size of the population had not changed appreciably since July.

In general, the population of the Check Area remained rather low, with only a 58.3 per cent increase during the breeding season of 1938. The area was closed to hunting during the fall of 1938, but the effect of this protection was insignificant, since the number of rabbits trapped in February 1939 was one less than in February, 1938. The peak population density for the two years was reached in May, 1939. Two months later (July), however, the number had decreased considerably. Migration, or predation by a marsh hawk probably was responsible for this decline. Evidently, the area had suitable cover for only about 2 adult female home ranges. At no time did the population reach a greater density than 1 rabbit to 10 acres of quadrat area.

ARTIFICIAL FOOD AREA

Nine rabbits (3 females, 6 males) were counted during late April, 1938. In late August, 1938, the population was 11 (juveniles: 3 females, 4 males; adults: 1 female, 3 males). Accordingly, only 2 more were present than during the previous spring. Only one of three females present during spring of 1938 was still there in the following August and the range of this one extended outside the area. Perhaps predation or emigration was responsible for the disappearance of the other two females.

The October, 1938, population was 16 (juveniles: 4 females, 5 males; adults: 3 females, 4 males). The three adult females taken were unmarked and two of them were never retaken. It is possible that two of these seemingly adult animals were large juveniles born early in 1938. The fall population was seven more than in the previous spring, an increase of 78 per cent.

At the beginning of the 1939 breeding season (March 1) only 7 (1 female, 6 males) were taken. This number does not differ significantly from those on the other areas at this season and was two less than present in April, 1938.

One hundred ten screen hoppers located grid fashion on the Food Area were filled with scratch feed on December 14, 1938, and were replenished throughout the winter until February 22, 1939 (Pl. 6, *B*). A supply of this food was constantly available to rabbits on the area throughout the winter, but the cottontails disappeared from the area except along the escarpment edge. A few individuals evidently were living in the adjacent bottomland, returning to the top of the escarpment to eat at the nearest feeders, and then returning to the lowland for cover. Allen (1939) found that cottontails regularly patronized feeding stations put out for birds. On the basis of the evidence here presented, however, it is concluded that an abundance of scratch feed in an area during winter will not necessarily increase the number of resident rabbits. Cottontails evidently will forsake an abundant supply of food for good cover, if the two are not found together.

The June, 1939, population was 9 rabbits (juveniles: 1 female and 1 male; adults: 6 females and 1 male). Three of the six adult females were unmarked, but the other three had been caught on the area previously.

During mid-July this area supported 21 rabbits (juveniles: 6 females, 7 males; adults; 8 females, no males). The population of breeding females on the area at this time was the largest noted there during 1938 or 1939. Two must have immigrated after June, 1939, at which time only six adult females were present. One of the immigrant females was released on an area one half mile distant in January, 1939. She roamed considerably during the breeding season, and did not appear to establish a fixed home range. No adult males were secured during the ten-day census, but it is almost certain that at least some of the four males taken in nine days of post-census trapping were residents, that had avoided capture during the regular census period.

During late October, 1939, 22 individuals (juvenile: 10 females, 12 males; no adults) were caught. This number is larger than at any other time during 1938 and 1939. The absence of adult rabbits of both sexes is unusual. Probably the majority, if not all, mature in-

dividuals had left the area, or avoided capture at this time. My supposition is that they had gone into the adjacent bottomland, which was used considerably by cottontails during the previous winter.

In general, cottontails of the Food Area did not remain to utilize the scratch feed during winter. A few fed at the stations near the edge of the escarpment, but were evidently occupying the bottomland coverts most of the time. The breeding population following the winter feeding was nine animals. They had benefited by protection from hunting the previous fall, and had access to an abundance of scratch feed during the winter of 1938–39. Despite this advantage, the 1939 spring population consisted of two fewer rabbits than during the spring of 1938. The late summer and fall population in 1939 increased, however, until late October when it was 37.5 per cent larger than during the fall of 1938. This increase in resident animals to one per 7.3 acres of quadrat area was correlated with increase in the number of breeding animals on the area in July, 1939, but cannot be traced to artificial feeding during the previous winter.

ARTIFICIAL BURROW AREA

During April, 1938, when first censused, 16 rabbits, (7 females, 9 males) were captured, the largest population on any management area during the spring of 1938. Two of the adult females had been released on the adjacent area (Stocking) two weeks previously. One adult male was taken for autopsy because of a mange-like condition of its skin, and one adult male was killed in a trap by a weasel.

On May 9 and 10, 1938, 112 artificial burrows were constructed and a month later rabbit hair was found in 36 burrows (32 per cent). Hairs found in the burrows were identified by the aid of a reference collection for field use (Haugen, 1939).

Between July 25 and August 6, 1938, 19 rabbits (juveniles: 5 females, 6 males; adults: 4 females, 4 males) were taken, three more than present during the previous spring. The actual increase, however, was five, because two of the spring residents were removed during that census. No signs of mortality were noted during the summer.

The fall population (November, 1938) consisted of 17 rabbits (juveniles: 5 females, 6 males; adults: 4 females, 2 males), one more than present the previous spring, but two-thirds of the population were juveniles. This lack of increase may have been due to mortality, excessive emigration, or in part to trap-shyness by adults in autumn.

During January, 1939, only 6 rabbits (3 females, 3 males) were taken. Part of the decrease may have resulted from an unknown amount of poaching just previously. Live-trapping at this time failed to capture a previously marked rabbit which was taken from one of the burrows during the census. Three other individuals taken from burrows two weeks previously were not retaken during the census, or on subsequent burrow checks. Each cottontail taken from burrows or by live-trapping in the area during January, 1939, had been eartagged during some previous census.

Artificial burrows were used by rabbits considerably between December 28, 1938, and January 27, 1939. During this time 9 cottontails (6 females, 3

males) were taken 12 times from ground dens. One of them was taken from one of two holes examined on January 25. All burrows were examined as a group five times during this period and the presence of rabbit tracks was considered as evidence that they had been used. On January 3, tracks of cottontails were found at the entrances of 33 (29.5%) of the 112 holes. Some burrows had beaten paths leading to the entrance, and it was not uncommon to find the tracks of a single animal entering two holes in one night.

At least six individuals occupied the Burrow Area during January, 1939, whereas the adjacent Stocking Area had only two. This difference in population was obvious both from trapping records and relative numbers of tracks. Where artificial burrows were accompanied by suitable cover and food (all-age stand of oak, with some underbrush), rabbits remained on the upland during winter. Ground holes located in the open or among large trees with a dense forest canopy were not used during winter because rabbits migrated from those localities. This evidence on the use of burrows according to location accords with that by Allen (1939) in southern Michigan.

During April, 1939, 12 rabbits (5 females, 7 males) were found on the Artificial Burrow Area. Six of them were also present in January; the others had evidently entered the area after the winter census. Four of the newcomers had been marked on the quadrat the previous fall but were absent during winter, and the other two were taken for the first time. The spring breeding population in 1939 accordingly was only three-fourths as large as that in 1938 (16 rabbits). Since two of the females in the 1938 spring census had immigrated soon after being released on an adjacent quadrat they probably should be disregarded in computing the population. Accordingly, there was an actual difference of only two rabbits in the spring populations of 1938 and 1939 (14 and 12 respectively).

Artificial burrows were used considerably and kept rabbits on the upland during the winter of 1938, and 1939, but did not bring about an increase in population during the following spring. Four juveniles were found in artificial burrows in May, 1939, but no adults were secured from burrows except during inclement winter weather.

In early August, 1939, 11 rabbits (juveniles: 4 females, 4 males; adults: 2 females, 1 male) were trapped, and during November, 1939, 14 were captured (juveniles: 6 females, 7 males; adults: 1 male). The catch of new individuals at this time was spread rather evenly over the entire census period. It appeared as if rabbits then were trapshy, but the actual cause of delay in captures is unknown. Such a delay makes a 10-day census appear incomplete. More cottontails, however, were on the area at this time than at any other time during 1939.

During July and August, 1938, more rabbits (one per 8.4 quadrat acres) were found on the area than at any other time, although the artificial burrows had been present for only two months.

The population of the Artificial Burrow Area was generally higher during 1938 than during 1939. This is surprising, because the breeding population of 1939 had been protected from legal hunting, and the burrows had held

several rabbits on the tract throughout the winter of 1938–39. During 1939, weasels on the quadrat increased and they frequently visited the live-traps, to kill or injure captive animals. At no time, however, was a rabbit known to have been killed in an artificial burrow. Burrows were readily used by cottontails as winter cover, but their presence did not increase the fall population available for sportsmen to harvest.

ARTIFICIAL STOCKING AREA

Thirteen rabbits (6 females, 7 males) were taken on this area in March, 1938, before any stocking was done. And then 11 additional rabbits (6 females, 5 males), live-trapped at the Mason Game Farm, were released on the plot. All appeared to be in good condition. The combined resident and released population at the end of March was 24 (12 females, 12 males).

In late July, 23 rabbits (juveniles: 9 females, 9 males; adults: 3 females, 2 males) were captured on the area. Four of the adults were local residents and the fifth was an introduced male. Seemingly, the other 10 introduced rabbits had left the area, were dead, or were avoiding capture. Of those introduced, two females and one male were recaptured on an adjacent area during spring and summer. Allen (1939) transplanted seven rabbits in an area under intensive study, and found that only one remained near the point of liberation. Of 51 mice (*Peromyscus leucopus noveboracensis*) which were moved 160 to 365 yards, Burt (1940) noted that only 2 per cent stayed at the point of release and 31⅓ per cent were not retaken again. Obviously then, the restocking of a given tract does not necessarily increase the future resident population of that area.

During November, 1938, 23 rabbits (juveniles: 7 females, 13 males; adults: 2 females, 1 male) were trapped. The plot was closed to hunting during the fall of 1938, consequently the population should have been normal.

In January, 1939, only two rabbits, a female and a male were trapped, and tracks were scarce. Unfortunately, the area had been illegally hunted by several men with two or more dogs on December 25, 1938. Very likely, several rabbits were bagged because most of the poaching occurred in the most densely populated part of the quadrat. Not all of the rabbits absent during the January census, however, had been shot. Some must have migrated from the area, because six from the fall population reappeared the following spring.

The population increased from 16 individuals in April, 1939, to 35 (juveniles: 14 females, 17 males; adults: 4 females) in August 1939. Eleven breeding females occupied the area during the spring. Four of these females were found pregnant 4 times; two, 3 times; two, 2 times; and three, 1 time during the 1939 breeding season. Undoubtedly, there were other pregnancies not detected among these females. If all known pregnancies had been successful, had been of average sized litters with complete survival, and had not dispersed previous to the August census, then 156 young should have been present at that season. If the population density of the surrounding area were equal to that in the area, dispersal probably would not have had much effect on the number of young present, because an equal number of young

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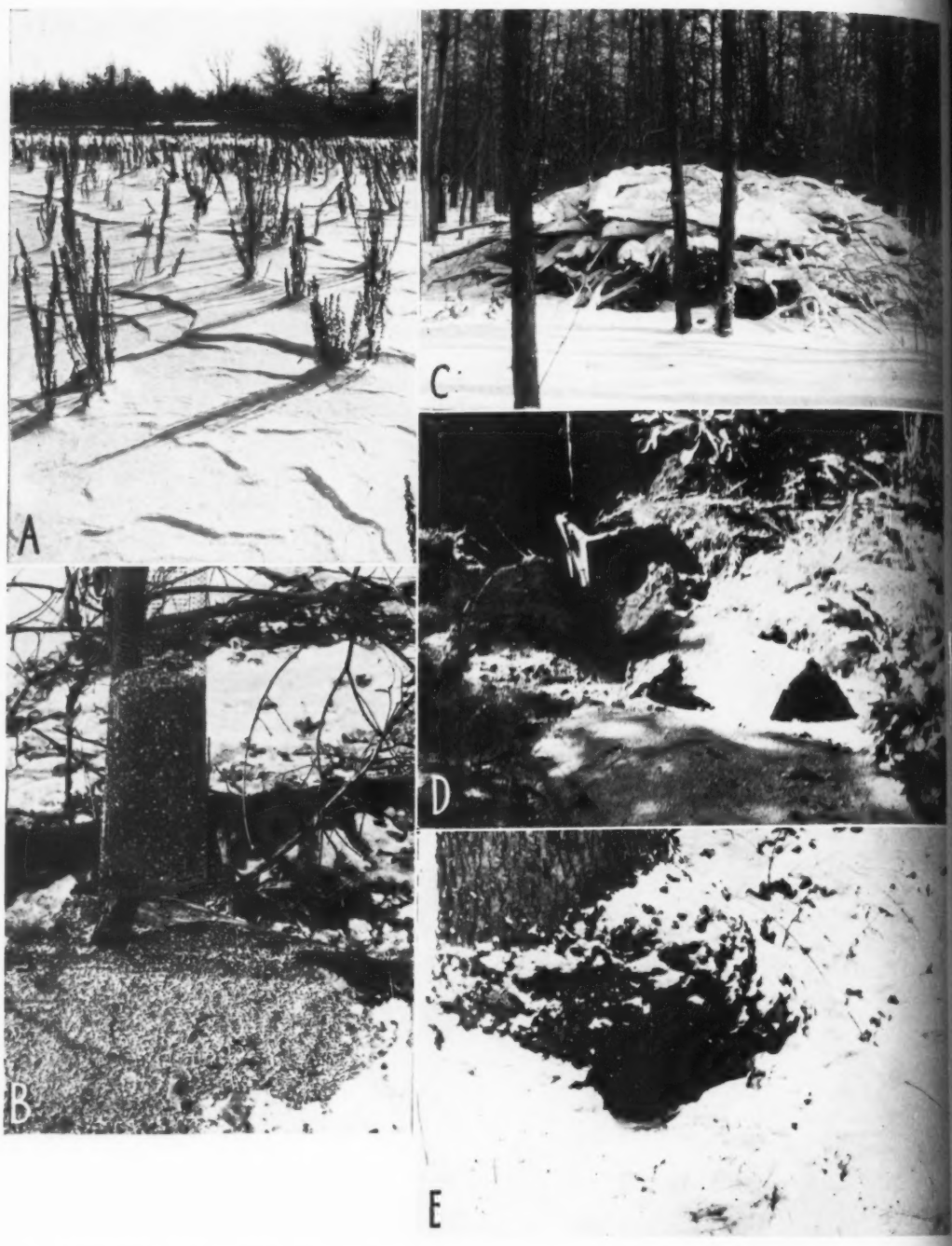
A. Grazed woodlot with browse line. Cattle have destroyed ground cover necessary to wildlife. *B.* Release cutting should be done in this stand of mature timber. *C.* Live-trap used in study. Traps covered with ½-inch hardware cloth are better and were used almost exclusively during the second year. *D.* Two years after this strip was cleared, the oak coppice and flowering dogwood were large enough to give good cover and food for cottontails. *E.* Pine planting frequented by cottontails more often than the dense-crowned stand of large oaks beyond. *F.* This dump forms excellent escape cover for cottontails.



A. Abandoned field covered with wormwood (*Artemisia caudata*). *B*. One of the 110 artificial feeding stations; much used by squirrels, and songbirds, some by opossums, but little by rabbits. *C*. One of the 112 brush piles constructed on the Brush-pile Area and used considerably by rabbits during inclement weather. *D*. Artificial burrow partially excavated by a canine predator. Such burrows were used considerably by rabbits during bad weather. *E*. Hole in base of white oak used by adult female cottontail during stormy weather.

PLATE 6

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ult female

would have left and entered the area. In August, there were 35 rabbits; the 31 young in this population indicate a possible known survival rate of only 1 young rabbit from 5 embryos.

In November, 1939, only 15 rabbits, all juveniles (10 females, 5 males) were taken, less than half the total present during August. This reduction probably resulted from emigration and mortality, as hunting was prohibited.

Liberation of 11 rabbits on the Stocking Area (13 known residents present at time) in March, 1938, did not significantly increase the numbers present during the following fall. Six subsequent censuses taken during the ensuing 19 months verify this conclusion. Poaching and migration helped to reduce the 1938 fall population until only two rabbits remained in January, 1939. Migrating animals repopulated the area during the spring of 1939. During the summer of 1939, the number increased to one and one-half (35 animals) that of the known summer population of 1938. The larger summer population in 1939 cannot be attributed to restocking in the spring of 1938. On the basis of the number of individuals present in 1939 and the known rate of reproduction of the breeding females taken on the area, it is believed that not over 1 rabbit in 5 survived until late August.

BRUSH-PILE AREA

When first censused in March, 1938, only 4 rabbits (1 female, 3 males) were taken. During April and early May, 1938, 112 piles (4½ ft. high and 12 to 14 ft. in diameter) were scattered at 110-yard intervals in a grid pattern throughout the area (Pl. 6, *C*). In June, 1938, a considerable increase in rabbits was noted, 14 individuals being present (juveniles: 1 female, 3 males; adults: 5 females, 5 males). The adult population apparently had more than doubled since March. The increase in breeding animals probably resulted from an influx of individuals during spring, and perhaps the newly constructed brush heaps had served as an attraction.

In late September, 14 were trapped (juveniles: 1 female, 9 males; adults: 2 females, 2 males), only two-fifths as many as present in June, but the juveniles had increased from four to 10. The population then was equal to that during June, but with an increased percentage of juveniles.

In December, 1938, only five were secured (juveniles: 3 males; adults; 2 males). Three of them had not been taken previously. The population had apparently decreased to about one-third the density in June and September.

On four occasions between December 23, 1938, and February 3, 1939 the brush piles were checked for signs of use. Cottontail tracks were found in or around 62 (55.4%) of the piles. During severe weather rabbits remained in the brush heaps except to venture out a few yards, feed, and then return to cover. During deep snow and stormy weather, eight rabbits fed outward from the pile for an average distance of 26.4 yards. In milder weather they often moved back and forth between 2 or more piles. Rabbit tracks were more numerous in this quadrat during the winter of 1938–39 than in any other study plot except the Artificial Burrow Area.

Where heaps of brush were available, a larger number of rabbits than usual

remained on the upland during winter. In February, 1939, 10 adults (2 females, 8 males) were taken on the Brush-pile Area. The preponderance of males taken indicates there may have been an influx of them. Adult males have a larger home range than do females, and it is therefore possible that more males found the added cover and remained to utilize the added security.

In May, 1939, 13 rabbits were taken (juveniles: 2 females, 2 males; adults: 4 females, 5 males), two more females and three fewer males than in February. The two new females were pregnant, and were probably residents of the quadrat.

A considerable reduction in population occurred between May 25 and July 10, 1939, at the end of which time only four rabbits (juvenile: 1 female; adults: 2 females, 1 male) remained. At this time, rabbits were taken in usual numbers in other study areas. Perhaps weasels or the pair of nesting broad-winged hawks contributed to the decrease in early summer population. A considerable amount of fur from juvenile rabbits was found beneath the hawk nest. The influence of these raptors probably decreased after July 20 when their young left the nest.

Between July and October, 1939, the population increased and 16 were taken during October (juveniles: 9 females, 4 males; adults: 3 males). This was the largest population found on the area in either 1938 or 1939. The increase in immature cottontails to 13 possibly was due to an influx of young, or to further reproduction by the two females present in July. In any event, the increase occurred after the departure of the nesting hawks, but the actual source of the fall population remains unknown.

In general, it appears that the average populations of the Brush-pile Area were comparable during 1938 and 1939 (brush piles constructed in May, 1938), except for the temporary reduction during July, 1939. The presence of weasels and a pair of hawks coincided with this temporary drop in population. No precise measure of predation, however, was secured. Brush piles were used considerably by the rabbits during inclement weather, and were undoubtedly instrumental in retaining a larger than average number on the area during winter; their ultimate effect on the population of huntable rabbits, however, remains uncertain.

DISCUSSION OF POPULATIONS

The data on populations for the five management areas in 1938 and 1939 are believed to be comparable. Major variations in the number of rabbits resulted from predation, migration, and poaching. The average number of cottontails on the five areas during 1938 increased steadily between June and November (Fig. 3), and was greatest from September to November.

During 1938 the management measures practiced were provision of artificial brush piles and burrows, and stocking. No subsequent increase in number of cottontails was noted during that year.

During the summer and fall of 1939, the populations on the areas were, on the average, not greatly different from those of 1938 (Fig. 3). A larger average number should have been expected in 1939, because, except for a little poaching, the study plots were not hunted in 1938. It is believed that the average

1939 fall populations would have been slightly higher if predation had not increased.

Irrespective of management measures, the greatest number of rabbits were among scattered growths of coppice and shrub reproduction. Rabbits were seldom noted in large open areas or in dense stands of mature timber with a complete forest canopy (Haugen, 1942b).

EFFECTIVENESS OF MANAGEMENT

Cottontails were scarce on the upland during winter because they migrated to the nearby lowland coverts. Many of the marked rabbits, however, reappeared on the upland in February and March. Where artificial burrows and brush piles were available along with moderately good tree and brush pile cover, the rabbits remained on the upland in greater numbers than in similar areas lacking this added artificial cover. Consequently, the addition of holes or brush piles reduced the concentration in the lowland coverts. Such concentrations ordinarily increase the vulnerability of rabbits to predation and to mortality by flooding. Considerable mortality by drowning of *Sylvilagus aquaticus littoralis* was found in Louisiana by Svihla (1929). Disease and parasitism, as well as vulnerability to predation are usually increased in importance among heavy concentrations of animals. Management measures which keep the rabbits dispersed on the upland should therefore be desirable.

Distribution of artificial food was not effective in retaining rabbits on the upland during winter. Instead, they seemed to withdraw into the bottomland at the advent of winter, although a few returned intermittently to eat the scratch feed provided. No evidence was found to indicate that artificial feeding was effective.

By introducing 11 rabbits on the Artificial Stocking Area of 160 acres in March, 1938, the potential breeding stock was raised from 13 to 24 cottontails. The following fall only 23 were present, indicating a failure in the restocking. The peak population of 35 there was found in 1939, during which year no cottontails were released. More breeding females, however, were present during 1939 than in the previous year. It is certain that this increased population did not result from restocking in the previous year, because most

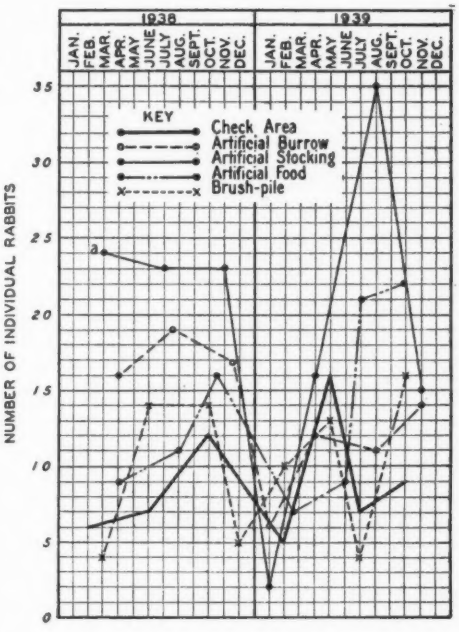

Fig. 3. Resident cottontail populations of six 160-acre management areas during 1938 and 1939; *a*, 13 resident and 11 transplanted; no further planting.

of the transplanted rabbits disappeared. The availability of better rabbit cover on the area was probably responsible for the greater number of rabbits than were found in the other areas of equal size.

COSTS OF MANAGEMENT

Employment of any management measure can be justified only when that measure so increases the population of the species managed that the value of the increase exceeds the cost of development. The latter value in one or more economically important species is intangible, and difficult to measure. Measures such as artificial burrows, stocking, winter feeding, and brush piles have been used in an attempt to evaluate their usefulness as management measures for cottontails.

Artificial feeding. Scratch feed consisting of 41 lbs. cracked corn, 34 lbs. oats, 13 lbs. wheat, 3 lbs. buckwheat, and 3 lbs. Kaffir corn was distributed on the Food Area during the winter of 1938–39. At an average value of $0.74 per bushel, the 53.62 bushels of feed distributed cost $39.68. Few cottontails remained on the upland to make use of the food and no increase in population resulted. Grouse, fox squirrels, deer, and songbirds used the feed extensively, but it is difficult to evaluate fully the ecologic effect of the feeding experiments for animals other than rabbits.

Brush piles. One hundred twelve heaps of brush (12 to 14 feet in diameter and about 4.5 feet high) were placed in the Brush-pile Area (Pl. 6, *C*). The foundations were made as follows: a log about 8 or 10 inches in diameter and 3 or 4 feet long was first placed and 5 or 6 longer and more slender pieces were radiated in spoke-like fashion from the center piece on which the inner ends rested. Brush was then placed over this circular or dome-shaped bottom structure. The 112 brush piles were constructed by a local W.P.A. project at the rate of one pile per 9 hours of labor. At the prevailing rates for W.P.A. labor each cost $3.28, and the expense of developing 160 acres was $367.36. If the piles remain useful for 6 years, the average annual cost is $61.23 per quarter section.

As previously noted brush piles retained more than an average number of rabbits on the upland during the winter and it is felt that their value should be further studied. From the cost of development and the scarcity of rabbits noted in this study, it is obvious that brush piles if used for cottontail management must be obtained as a byproduct of wood cutting, or by volunteer labor. Timber cutting in addition to providing brush heaps leads to and increase in shrubby vegetation where rabbits are most abundant (Haugen, 1942b).

Artificial burrows. One hundred twelve artificial burrows were constructed from scrap lumber and placed within a 160-acre area. Each consisted of a 54-inch tunnel and a nest box. The tunnel was made from two 8-inch boards, nailed together along one edge to form an inverted trough, which was buried in a trench (Pl. 6, *D*). The entrance end was level with the ground surface and the lower end opened into the nest box 18 inches below the surface. The nest box was 12 inches square by 18 inches high, with a removable lid resting on cleats at a point 6 inches below the top of the box. The nest

box was set into the ground so that its top end was flush with the surface.

The 112 burrows were constructed and buried at a labor cost of $0.47 each. The cost of developing 160 acres was therefore $52.64 (144 man-hours of labor). If the burrows last 4 years, the average annual cost of development would be $13.16. This may be too high to be practicable but more nearly approaches a reasonable figure than did that of development with brush piles.

Artificial stocking. Eleven rabbits were released on the Stocking Area in late March 1938. Gerstell (1939) found the cost of capturing, transporting, and releasing local cottontails in Pennsylvania to be $0.35 each. At this rate, the restocking of 11 rabbits probably cost a minimum of $3.85. This expense seems reasonably low, but the release of cottontails had little or no effect on the ultimate population the following fall. A second remote area was stocked with 68 wild cottontails with no resulting increase in the local population (Haugen, 1941). Such findings are in agreement with the observations of Gerstell (1937) in Pennsylvania. As a rule, the released rabbits roamed considerably, and they may have caused a small increase in the general population of the region, although such an influence was not detected.

GENERAL DISCUSSION

Female cottontails in Michigan often produce four litters in a season and each litter averages 5.4 young (Haugen, 1942b), so that one female may bear 20 or more young per season. Factors other than reproductive rate therefore, must limit the cottontail populations in the region.

Competition for home sites or territories by adult breeding females may at times limit cottontail populations. The areas studied usually contained some apparently suitable habitats in which breeding females were not taken, so that there seemed to be an excess of available home sites (Haugen, 1942a). It seems, therefore, that the cottontail populations studied were not limited to any great extent by competition for nesting sites. Females and young which occupied the least favorable habitats probably suffered the greatest mortality by predation, as such habitats averaged fewer rabbits than more favorable ones.

The main factor limiting cottontail populations on the study areas under present conditions of food and cover is evidently mortality, and not emigration or inadequate reproductive rate. Intensive study of the Stocking Area revealed that most of this mortality was among juveniles; only about one young in five survived until fall. It is not known that disease or parasites caused any appreciable loss among the local wild cottontails; on the contrary, heavily parasitized individuals often appeared fat and healthy. In this study, the only two known deaths from disease were among captive rabbits. Tularemia has not yet been found in the vicinity of the station.

Migration of cottontails to the lowlands, for cover and the resultant concentration there during winter probably increased mortality by predation. The population on an area supplied with a superabundance of artificial food migrated similarly. Rabbits on areas developed with brush piles, and with artificial burrows, however, did not

migrate so readily, but remained to utilize such cover.

Predator pressure is evidently exerted throughout the year, but no precise measure of predation was obtained. The area seemed to have a predator population slightly greater than the average in southern Michigan.

The upland soil is sandy and poor, producing little succulent food and cover. The growth of these necessities is further limited by a lack of sunlight, screened out in many places by a dense forest canopy. As a result of food and cover deficiency the sandy upland areas are little used by other prey species such as ground squirrels (*Citellus*) and chipmunks (*Tamias*). Woodchucks and skunks are only occasionally present and meadow mice (*Microtus*) were not taken on the upland. Accordingly, the cottontail, opossum, fox squirrel, and wood mouse (*Peromyscus leucopus*) probably bear the brunt of predation. Opossums and other species may also feed on young cottontails still in the nest. The scarcity of woodchucks and skunks on the upland also handicaps rabbits because of the resulting lack of burrows for winter use.

Because of the insufficiency of other prey species and escape cover, the cottontail apparently is preyed upon heavily. Rabbits are mainly dependent upon their ability to flee for survival from attacks by predators and it is vitally necessary that they have access to a variety of well dispersed cover. Access to such cover is especially needed by juveniles which are inexperienced in escape and more easily captured.

To provide adequate cover for cottontails on submarginal land with extensive stands of timber, the growth of brush and succulent herbs could be promoted by small release cuttings (plots of 1 to 2½ acres may be desirable). Large idle fields probably can be improved by a network of strip and spot plantings of pines and shrubs. Such plantings have already been made at a state game area in southwestern Michigan, where about 453,000 trees and shrubs have been planted since this study was completed. Most plantings are irregular strips which meander about over contours to connect existing coverts. An average distance of about 150 to 200 yards between strips (3 or 4 rods wide) and spot plantings seem preferable because rabbits did not utilize wider open areas devoid of nearby escape cover. Such strip and spot plantings provide considerable forest edge which permits cottontails to utilize a greater amount of area, yet be reasonably close to adequate escape cover. As a supplement to such woody cover, sweet clover is excellent (Haugen, *MS*).

Good results in survival have been obtained in southern Michigan on the W. K. Kellogg Bird Sanctuary with local wildlife plantings using false indigobush (*Amorpha fruticosa*), grape (*Vitis* sp.), coralberry (*Symphoricarpos vulgaris*), privet (*Ligustrum ibota*), honeysuckle (*Lonicera morrowi*, *L. tartarica*), snowberry (*Symphoricarpos racemosus*), black locust (*Robinia pseudoacacia*), buckthorn (*Rhamnus cathartica*), and red mulberry (*Morus rubra*) (Haugen, *MS*). The bark of false indigobush and sumac are preferred winter food for cottontails at the Sanctuary.

Where possible, the presence of such burrowing animals as woodchucks, skunks, and badgers should be encouraged. Combinations of two or more

of the above mentioned "natural" management measures will afford rabbits a more secure habitat in which to live, and will prove more permanent and economical than attempts to control predators.

LITERATURE CITED

ALLEN, D. L. 1938. Ecological studies on the vertebrate fauna of a 500-acre farm in Kalamazoo County, Michigan. Ecol. Mon., **8**: 347–436.

1939. Michigan cottontails in winter. Journ. Wildl. Mgt., **3**: 307–322.

BOLE, B. P., JR. 1939. The quadrat method of studying small mammal populations. Cleveland Mus. Nat. Hist., Scient. Publ. **4**: 15–77.

BURT, W. H. 1940. Territorial behavior and populations of some small mammals in southern Michigan. Univ. Michigan, Mus. Zool. Misc. Pub., **45**.

DICE, LEE R. 1938. Some census methods for mammals. Journ. Wildl. Mgt., **2**: 119–130.

FIPPIN, E. O. and T. RICE. 1901. Soil survey of Allegan County, Michigan. U. S. Dept. Agric., Bur. Soils, Rept., **3**: 93–124.

GERSTELL, RICHARD. 1937. Management of the cottontail rabbit in Pennsylvania. Pa. Game News, **8**(1): 16–19.

1939. A progress report on Pennsylvania's new rabbit program. Pa. Game News, **10**(3): 4–5, 31.

HAUGEN, A. O. 1939. Technique for preparing a hair collection for field or laboratory use. Jour. Mammalogy, **20**: 260.

1941. Life history and management studies of the cottontail rabbit in southwestern Michigan. Univ. Michigan Graduate School. MS Thesis.

1942a. Home range of the cottontail rabbit. Ecology, **23**: 354–367.

1942b. Life history studies of the cottontail rabbit in southwestern Michigan. Amer. Midl. Nat., **28**: 204–244.

Wildlife plantings at W. K. Kellogg Sanctuary and farm. MS report to Mich. Dept. Conservation.

LEVERETT, FRANK. 1917. Surface geology and agricultural conditions of Michigan. Mich. Geol. and Biol. Surv., Pub. 25, Geol. Ser., **21**: 1–223.

SVIHLA, R. D. 1929. Habits of *Sylvilagus aquaticus littoralis*. Jour. Mammalogy, **10**: 315–319.

TRIPPENSEE, R. R. 1934. The biology and management of the cottontail rabbit. Univ. Michigan School of Forestry and Cons., MS Thesis.

VEATCH, J. O. 1933. Agricultural land classification and land types of Michigan. Mich. Agric. Exp. Sta., Spec. Bul., **231**: 1–51.

CHAPARRAL CROWN SPROUTS AS BROWSE FOR DEER

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There is vigorous sprout growth in some species of the California chaparral[1] when the plants are killed back to the ground level by cutting or burning. This is browsed eagerly by black-tailed deer (*Odocoileus hemionus* ssp.) through a good part of the year. The deer tend to concentrate on this browse to such an extent that hunters consider burned or lopped areas of sprouting brush ideal for bagging their deer. If crown sprouts

[1] "Chaparral" refers to all the "hard" brush plants characteristic of the brushland association at intermediate elevations in California. It occupies about 7 per cent of the state as an almost unbroken belt in the lower levels of the coast mountains and Sierra Nevada. Extensive areas of this association support a sprouting form of brush.

could be produced in sufficient amounts to favor deer populations on such areas without injury to other values, the economic status of these lands would be enhanced, as much of the region is clearly submarginal for agricultural purposes. This paper suggests some of the reasons why deer favor burned areas of sprouting brush, points out the effect of repeated browsing upon sprout growth, and considers the application of such knowledge to deer management on chaparral lands.

COMPARATIVE NUTRITIVE VALUES

During the late summer of 1940, samples of closely-browsed crown sprouts of slashed chamise (*Adenostoma fasciculatum*) were collected for chemical analysis, with samples of current growth stages of uncropped plants (Table 1). Chamise was selected because it dominates large expanses of brushland in California.

Table 1.—CHEMICAL COMPOSITION OF CURRENT GROWTH OF CHAMISE FROM LAKE COUNTY, CALIFORNIA (*Percentages of oven-dry weight*).

	Young crown sprouts	*Leafy stems, full bloom*	*Leafy stems, seeds forming*	*Leafy stems, seeds formed*
Silica-free ash	6.16	2.87	3.11	1.79
Calcium	1.26	0.51	0.65	0.38
Phosphorus	0.55	0.19	0.17	0.08
Ca:P ratio	2.3	2.7	3.8	4.7
Crude protein	17.53	7.41	6.03	2.89
Crude fiber	12.89	16.78	18.54	28.71
Moisture content	130	65	50	39

These data show that succulent crown sprouts afford higher nutritive values than samples of the current but older, uncropped growth stages, having at least twice as much water, minerals, and crude protein per unit of total dry weight, besides a lower calcium:phosphorus ratio, and lower percentage of crude fiber. From the standpoint of animal nutrition these differences seem to be in favor of the browsed crown sprouts.

EFFECT OF BROWSING ON NUTRITIVE VALUE

Repeated close browsing of crown sprouts by deer appears to retard the normal seasonal development of the shrubby tissues toward maturity. Gordon and Sampson (1939), Hart and associates (1932), and Hellmers (1940) have reported that browse plants undergo conspicuous nutritional declines with change from young to older growth stages. The sharp decline in crude protein content of sprouting brush with advance of the season to older growth stages is illustrated in Figure 1, adapted from studies by Sampson (*MS*).

Since browse is less desirable to deer in older growth stages, close browsing of sprouts produces two reactions with respect to the deer: the nutritional quality of the forage is improved (Table 1), and the period of desirable browse is lengthened. These two desirable conditions, however, do not necessarily continue, year after year, on burned or slashed areas. The deer benefit because of the higher nutritive value and prolonged palatability of crown sprouts but the regenerative power of the plants declines until they die if sprouts are browsed too frequently and closely (Pl.

7, *C*), as any plant repeatedly deprived of its photosynthetic parts is unable to store sufficient food reserves, and eventually dies (Miller, 1938). Continued close cropping by deer may be an effective means of clearing small burned areas of sprouting brush (Sampson, *MS*).

WHY DEER EAT CROWN SPROUTS

It is problematical why deer favor areas of burned or slashed brushland, which produce abundant crown sprouts, since little is known about the physiology or "psychology" of food selectivity in these or other herbivores. To offer speculation water is likely the first limiting factor in normal animal metabolism (Maynard, 1937), so that the moisture content of young sprouts would favor their greater paltability to deer as compared with more mature plants of chamise or other chaparral. During the hot, dry summers in California chaparral, the succulent sprouts may be sought solely because of their higher moisture content. Associated with the high water content are, however, high levels of both organic and inorganic constituents important in animal nutrition. This relationship may combine to increase the desirability of the chaparral sprouts. Some factors not here measured may influence or even dominate the selective feeding habits of deer. Possibly some aromatic oil, more abundant in the younger growth stages, may attract deer.

MANAGEMENT SUGGESTIONS

Many species other than chamise in the California chaparral are browsed by deer and sprout from root crowns when the plants are burned or slashed. The more important of these include: madrone (*Arbutus menziesii*), Lemmon ceanothus (*Ceanothus lemmoni*), Parry ceanothus (*C. parryi*), blueblossom (*C. thyrsiflorus*), California coffeeberry (*Rhamnus californica*), California snowdrop berry (*Styrax officinalis* var. *californica*), chokecherry (*Prunus demissa*),

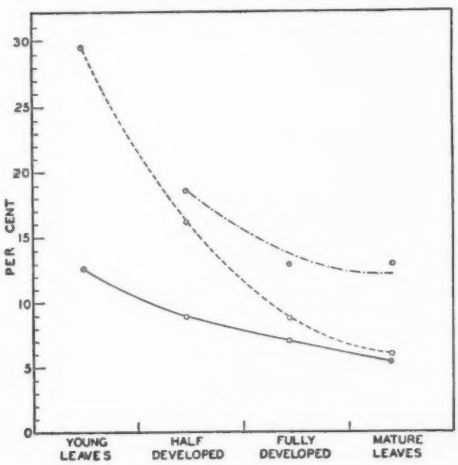


Fig. 1. Trends in crude protein of sprouting browse species of chaparral from early spring to end of growing season. —, chamise; – – –, poison oak; – · – · –, coffee berry.

and certain manzanitas (*Arctostaphylos* spp.). These, with chamise, comprise much of the hard-brush association of California (Pl. 7, *A*).

The hard-brush belt is a favored habitat of resident deer and serves further as a haven for those from the higher mountains during the months when the latter areas are uninhabitable. Accordingly, the investigation suggests a possible means of providing increased foraging grounds. If small, rather widely spaced areas of crown sprouts were provided on suitable chaparral areas, both migrant and resident deer populations might be benefited. These would have

to be judiciously selected and new areas would have to be provided intermittently if such a management procedure is to be successful. Newly burned or slashed areas would be necessary every two or three years, since in that time crown sprouts either become so dry and unpalatable as to be undesired by deer, or the plants are killed by too close use. More investigation is needed before specific recommendations can be made as to the wisdom of adopting plans to provide such foraging grounds. Any areas burned or slashed to increase forage for deer should provide water within a reasonable distance, should be selected to afford adequate escape cover, and should not be subject to excessive erosion when the protecting vegetation is thinned or removed.

Areas other than the chaparral belt of California may also be converted to valuable deer foraging grounds, if they support sprouting vegetation palatable to deer. The sprouts of various hardwoods have been reported to be sought for by white-tailed deer (Krefting, 1941) because of increased availability, and perhaps also increased succulence. The present investigation has given reasonable assurance that such fresh sprouts are also higher in nutritional values than the current growth of undisturbed plants. Thus, on areas where availability of forage for deer becomes acute during winter and early spring, a twofold purpose is attained by making provisions for crown sprouts.

SUMMARY

Black-tailed deer in browsing tend to favor areas of brush with an abundance of young, succulent crown sprouts. These have a higher nutritional content than older growth stages of the same plants, and continuous cropping by deer keeps the sprouts in younger growth stages. Accordingly, the deer are instrumental in producing a desirable food supply for themselves, once crown sprouting has been induced. The sprouts are, however, subject to limitations; if browsed too closely the plants are killed in a few years, and if not browsed enough the shoots soon become harsh and unpalatable, and then are not sought by deer. A management technique is suggested for benefiting deer on chaparral and other areas, affording a palatable vegetative cover which sprouts when cut or burned.

LITERATURE CITED

GORDON, A., and A. W. SAMPSON. 1939. Composition of common California foothill plants as a factor in range management. Calif. Agr. Exp. Sta. Bul. 627: 1–95.

HART, G. H., H. R. GUILBERT, and H. GOSS. 1932. Seasonal changes in the chemical composition of range forage and their relation to nutrition of animals. Calif. Agr. Exp. Sta. Bul. 523: 1–62.

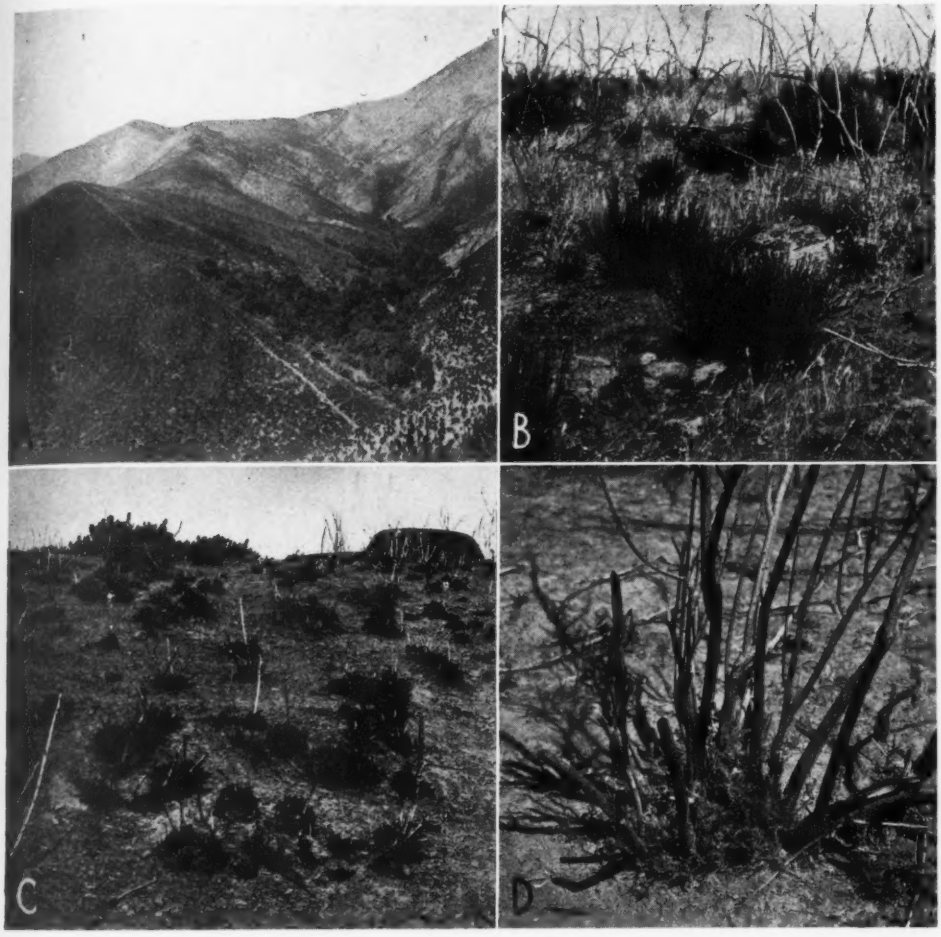
HELLMERS, H. 1940. A study of monthly variations in the nutritive value of several natural winter deer food. Journ. Wildl. Mgt., 4: 315–25.

KREFTING, L. W. 1941. Methods of increasing deer browse. Journ. Wildl. Mgt., 5: 94–101.

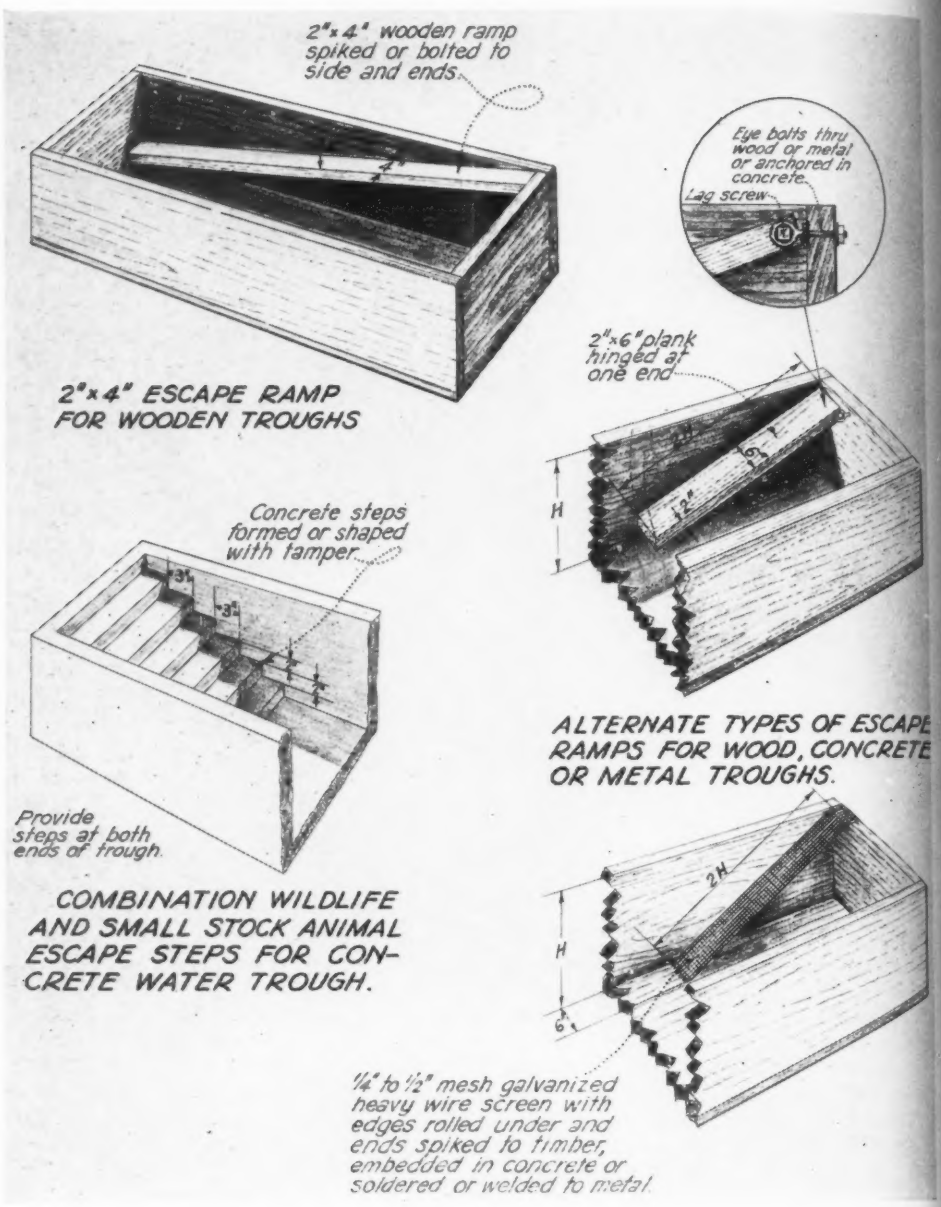
MILLER, E. C. 1938. Plant physiology. 2d ed. New York, McGraw-Hill Book Co., 1132 pp.

MAYNARD, L. A. 1937. Animal Nutrition. New York, McGraw-Hill Book Co., 461 pp.

SAMPSON, A. W. 1942. Plant succession on burned chaparral lands in northern California. (MS).



The chaparral association of California, predominantly chamise, is an important feeding ground of black-tailed deer. *A*. Chamise-covered hills. *B*. Chamise area burned two years previously, showing vigorous crown sprouts. *C*. Area of chamise sprouts produced after burning, and closely browsed by deer. *D*. Chamise crown sprouts cropped closely by deer.


2"x 4" wooden ramp spiked or bolted to side and ends
2"x 4" ESCAPE RAMP FOR WOODEN TROUGHS
Eye bolts thru wood or metal or anchored in concrete
Lag screw
2"x6" plank hinged at one end
6"
12"
H
ALTERNATE TYPES OF ESCAPE RAMPS FOR WOOD, CONCRETE OR METAL TROUGHS.
Concrete steps formed or shaped with tamper
3"
3"
Provide steps at both ends of trough
COMBINATION WILDLIFE AND SMALL STOCK ANIMAL ESCAPE STEPS FOR CONCRETE WATER TROUGH.
2H
H
6"
¼" to ½" mesh galvanized heavy wire screen with edges rolled under and ends spiked to timber, embedded in concrete or soldered or welded to metal

Escape ramps and steps for stock-watering troughs.

SCAPE
CRETE

BRIEFER ARTICLES

RAMPS FOR ESCAPE OF WILDLIFE FROM STOCK-TROUGHS

Straight-sided watering troughs for stock in arid country are often death traps for small birds and mammals, especially when algal growths at the surface give a false appearance of solidity. I have seen many examples of such needless destruction. On Santa Barbara Island off the California coast there is an old, concrete storage tank in which a dozen or so small birds, mostly Gambel sparrows and house finches, drowned daily in April and May when there was no other free water available. A stock trough in Clark County, Nevada, contained fur, feathers, and tracks showing that numbers of small birds, quail, and *Peromyscus* drowned, most of which had been removed by coyotes and eaten on the spot, so that the water did not become badly fouled. In a stock trough in Lincoln County, Nevada, I found recognizable remains of six jack rabbits, two cottontails, one adult Gambel quail, and 11 Nevada sage sparrows; the water was foul and unfit for stock.

Most of these creatures would have escaped, if some simple type of escape ramp had been provided. All stock troughs built or planned by the Soil Conservation Service in California or Nevada incorporate such devices. Suggested types are shown in Plate 7, but these designs need not be followed exactly. The essential requirement is a durable ramp attached so that it cannot be removed or broken by stock or man, at least without some effort. It must be at least 4, and preferably 6 or more, inches wide and roughened or on a gradual slope to afford foothold for birds, squirrels, rats, and rabbits. The slope should never be steeper than 1½:1 and the ramp must work as well when the tank is nearly empty as when it is full. Such devices not only will save the lives of many small birds and mammals, but will also prevent water from becoming foul and unfit for stock use, they possibly will also help to prevent spread of certain stock parasites of which the small creatures may be alternate hosts.—RICHARD M. BOND, *Soil Conservation Service, Berkeley, California.*

COUNTS OF BUCKS VS. SHED ANTLERS IN ROCKY MOUNTAIN MULE DEER

Big-game managers wish to maintain the quality of their breeding stock, especially where selective hunting prevails through the application of buck or bull laws. The hunting of males only may eliminate animals with the more desirable or "trophy" heads and, where spike bucks are legal game, excessive killing of these less wary animals may occur under heavy hunting pressure. Information on the herd composition should be obtained to learn the effect of these types of harvest.

It is seldom possible to make adequate field observations on antler classes when the deer are concentrated on winter range, as some inaccessible areas are seldom visited. Moreover, records must normally be obtained before mid-January, as the antlers are usually shed soon thereafter. Some workers have made collections of shed antlers as an indirect means of getting the desired information, but this is only practicable when a large representative collection can be made without undue expenditure of time.

During the winters of 1939–1940 and 1940–1941, we had an excellent opportunity to compare actual counts of bucks and of shed antlers in Rocky Mountain mule deer (*Odocoileus hemionus*) at Sapinero, Gunnison County, Colorado. The area was very accessible, especially where State feeding stations were located, and it was comparatively easy to obtain data on antler classes. Previous studies had shown that each band of deer was rather definitely confined to a certain drainage basin or feeding ground.

Six areas were selected for study. Prior to

Table 1.—COMPARATIVE COUNTS OF MULE DEER BUCKS AND COLLECTIONS OF SHED ANTLERS.

Points[a]	1939–40				1940–41			
	Bucks		Shed Antlers		Bucks		Shed Antlers	
	No.	%	No.	%	No.	%	No.	%
1	28	(8)	18	(5)	20	(6)	10	(3)
2	76	(22)	81	(23)	95	(28)	65	(21)
3	87	(25)	87	(24)	86	(25)	96	(32)
4	135	(39)	149	(42)	122	(35)	122	(40)
5	13	(4)	12	(3)	17	(5)	6	(2)
6	11	(3)	11	(3)	6	(2)	6	(2)
Total	350		358		346		303	

[a] 2-point bucks include 1×2 and 2×2; 3-point bucks, 2×3 and 3×3, etc.

the shedding season, careful counts were made of the antlers borne by a portion of the herd in each selected drainage. This usually was done on or near a feed ground. Records considered in the analysis were limited to those bucks accurately identified as to antler classes. Shed antlers were collected after such areas were free from snow in the spring and restricted to currently shed antlers from the same areas used for the actual counts. Each antler was recorded according to the number of points. Consequently, the shed antler tabulation is double the number of bucks involved.

The groups of shed antlers, by percentages, compare closely with the actual counts of deer (Table 1). A lower percentage of the shed 1-point or spike antlers would be expected, as they are more likely to be overlooked in the ground cover than the larger sizes.

The method should be tested further, especially under natural conditions, away from feeding stations, but it indicates that fairly accurate antler class groupings of a deer herd can be obtained by collecting and tabulating the recently shed antlers.—M. R. HICKEL AND LLOYD W. SWIFT, *U. S. Forest Service, Denver, Colorado.*

RELATIONSHIP OF FOREST WILD LIFE TO PINE REPRODUCTION

A recent survey of the literature supplemented by field observations has indicated that some of the most important eaters of pine seed have not always been recognized. It may, therefore, be of interest to point out some of the smaller forms of wildlife that feed on three species of western pines which form an important lumbering, recreational, and water-shed resource. Much remains to be discovered concerning the place of mice and chipmunks in relation to reforestation and forest maintenance. Seeds of most pines are taken eagerly by most mice and by the more apparent seed eaters such as squirrels. Other rodents and small birds also enter this complicated relationship to an extent that is not fully understood. The lists of species presented here are not complete, but they serve to indicate the scope of small forms of wildlife in relation to pine seed, and undoubtedly will stimulate other persons to record available field data on the subject.

Species reported to have eaten seed of the western yellow pine (*Pinus ponderosa*): sierra grouse (*Dendragapus fuliginosus sierrae*), ruffed grouse (*Bonasa umbellus*), California quail (*Lophortyx californica*), band-tailed pigeon (*Columba fasciata*), red-shafted flicker (*Colaptes cafer collaris*), Lewis woodpecker (*Asyndesmus lewis*), Steller jay (*Cyanocitta stelleri*), evening grosbeak (*Hesperiphona vespertina*), pine grosbeak (*Pinicola enucleator*), red crossbill (*Loxia curvirostra*), red-backed junco (*Junco caniceps dorsalis*), Mexican junco (*Junco phaeonotus*), western gray squirrel (*Sciurus griseus*), red squirrels (*Tamiasciurus douglasii*), ground squirrels (*Citellus columbianus, C. beecheyi fisheri, C. lateralis, C. l. chrysodeirus*), chipmunks (*Eutamias amoenus, E. minimus, E. cinereicollis*), pocket mouse (*Perognathus parvus*), kangaroo rat (*Dipodomys heermanni*), and white-footed mouse (*Peromyscus maniculatus*).

Species reported to have eaten seed of Jeffrey pine (*Pinus jeffreyi*): California quail (*Lophortyx californica*), red shafted flicker (*Colaptes cafer collaris*), crow (*Corvus brachy-*

rhynchos), Clark nutcracker (*Nucifraga columbiana*), western gray squirrel (*Sciurus griseus*), red squirrel (*Tamiasciurus douglasii*), California ground squirrel (*Citellus beecheyi fisheri*), chipmunks (*Eutamias amoenus, E. minimus, E. quadrivittatus, E. speciosus, E. townsendii*), kangaroo rat (*Dipodomys heermanni*), white-footed mouse (*Peromyscus maniculatus*).

Species reported to have eaten seed of the sugar pine (*Pinus lambertiana*): Clark nutcracker (*Nucifraga columbiana*), western gray squirrel (*Sciurus griseus*), red squirrel (*Tamiasciurus douglasii*), chipmunks (*Eutamias quadrivittatus, E. speciosus, E. quadrimaculatus*), white-footed mice (*Peromyscus maniculatus*).—CLARENCE F. SMITH, *U. S. Fish and Wildlife Service, Mount Shasta, Calif.*

OBITUARY

P. S. LOVEJOY[1]

The parentage of ideas about egg-openers, iceboxes, and cigarette-lighters is recorded in the United States Patent Office. Inventors are lauded in every schoolroom, and encouraged to levy tribute on all who use their intellectual progeny. The parentage of ideas about men and land is seldom recorded at all. By the time they appear in books they are usually step-children whose parentage has been forgotten.

I believe that P. S. Lovejoy sired more ideas about men and land than any contemporary in the conservation field. I here attempt to sketch some recent and unpublished chips from the Lovejoy block. Only a fraction of his output ever reached print. Much of it is recorded only in letters, and these are couched in a vernacular peculiar to him. In my office, and I fancy in many others, the arrival of a letter in Lovejoyeese was always heralded by titters from the mail room. My file of Lovejoyiana shows that this vernacular grew in extravagance and in wit as its contents deepened with advancing age. Why did he, a master of the Queen's English, insist on expressing even the most profound ideas in this jargon? It represents, I think, reaction against pretense, and a contempt for all pious solemnities.

No greater error could be made than to regard the Lovejoy vernacular as mere slang; it often carried figures of speech of poetical beauty. Two years ago, after he had recovered from an almost fatal illness, I remarked, in reply to a brilliant satirical letter (9/14/40), that I was glad he had resumed his mental probings into the nature of things. He replied: "I've been living on borrowed time. It's fun now to work up wedge-stuff, and find season-checks to set 'em in, and keep splitting more and more slabs of savvy off the bug chunk." Slang, yes, but also a pro-

[1] Parish Storrs Lovejoy was born at Princeton, Illinois, January 23, 1884 and died at Ann Arbor, Michigan, January 20, 1942. His ancestors on both sides were ministers and educators.

In 1903 he enrolled as one of the first students in Filibert Roth's School of Forestry at the University of Michigan. Before obtaining a degree, he entered the U. S. Forest Service in 1905, and became Supervisor of the Medicine Bow National Forest in Wyoming. In 1910 he was transferred to the Olympic National Forest in Washington and in 1912 returned to become Assistant Professor of Forestry under Dr. Roth at Ann Arbor. In 1920 Lovejoy became a staff writer for the Curtis publications, and had frequent articles on land-use, mainly in "The Country Gentleman." He helped to organize the Michigan Land Economic Survey in 1922, and took charge of it the following year for the Michigan Conservation Department. This led to the establishment of the Michigan refuge system, which Lovejoy undertook in 1925. He became chief of the Department's Game and Fur Division in 1927. After 1930 failing health forced him to relinquish active field work, but he continued to serve as advisor to the Department on land policy and program.

He married Ruth Harrison of Detroit in 1909, and is survived by his wife, a son, and three daughters. On June 7, 1942 a bronze tablet commemorating his services to conservation was dedicated on Pigeon River State Forest, one of his favorite areas, and a monument in itself to his labors.—*P. S. Hoffmaster.*

found and dramatic definition of scholarship, rendered in the mental imagery of the lumberjack.

I once upbraided "P. S." for not publishing more papers. I told him he was like a squirrel who buried his mental garnerings in letters, instead of planting them in print where they could grow in many minds. He replied: "I've been watching those squirrels. They don't even try to remember where they put acorns. They just cache them all over the neighborhood, and then go and smell 'em up again, as wanted. The squirrel that plants an acorn is not always the one to smell it up. Meanwhile quite a lot of them have sprouted and grown into trees. Caching things in print is not always the best way to get things *growing*" (letter 9/14/40). In this homely parable is compressed his own picture of his service to society.

Lovejoy's early writings dealt with physical resource problems, and with land policy. The deflation of the lake states land boom, the recognition of forestry by the agricultural profession, and the realization that forest lands as well as farm lands may be submarginal are in no small degree Lovejoy's personal handiwork. He also contributed largely to the recognition of wildlife as a land crop, and to the initiation of wildlife research.

In his later years, his thinking focused not on policy, but on people. He saw that the average citizen had given nothing but lip-service to either forestry or wildlife management, and he wanted to know why. Unlike most publicly employed conservationists, he did not mistake the growth of appropriations and the proliferation of bureaus for the accomplishment of the ends for which they were created. He became engrossed in analyzing the reasons for the failure of "conservation education."

His findings are expressed in "Ecological Engineering." I consider this one of the most important papers on conservation published during the current decade, but like other Lovejoy "acorns," it was cached at random in an obscure spot.

ECOLOGICAL ENGINEERING

Conservation, Lovejoy says, is reason applied to environment. Reason, to the mass mind, is like oxygen to the animal body: a little is essential, but too much is toxic, and induces pain followed by defensive reactions. Tolerance for reason may be increased by education, but only by slow degrees. Agricultural extension has developed techniques which recognize the limits of public tolerance; it administers small doses of "science" heavily diluted with economic and social persuasion. Conservation must do the same.

Lovejoy's distinction between educator and extensionist is elaborated in a recent letter (3/8/39):

"Educators smear all behaviors which are not dominantly rational. The standard campus illusion is that *Homo* can and should be educated so that he will not much, if any, (or anyway not in public) behave like a mammal. All the while everybody knows he will.

Skillful advertisers, politicians, and evangelists know in advance that most of the time people will react to stimuli and inhibitions which have little or nothing to do with the campus formula.

The extensioner splits the difference. He does not expect his customers to be much or often rational. He uses fact-logic only when it seems to work. When it doesn't work, he contrives bait and drift-fences and banana-peel arrangements which do. His job is to bridge the gap between the latest Experiment Station dope and the specific action-program. When the educator has done his stuff, the customer is due to be intelligent, but the extensioner is content if he thereafter acts as if he were."

I add from "Ecological Engineering":

"It is an almost universal assumption that there is something pathological in politicians. This, assuredly, is a misconception. The politician has always been associated with civilization, and has a function corresponding to that of leucocytes in the blood. The splitting of differences of interest among the governed is a perennial job. Our ecological engineer may be glad to have someone tending the minor chores while he himself is computing another social modulus, or triangulating to place another banana-peel where it will do the most good. Our engineer will bear in mind that *Homo sapiens* is still considerably sap. The normal function of the politician is to take the public where he thinks it wants to go; the function of our engineer is to take the public where it will be glad to be when it gets there.

Testing his materials in advance of construction, a proper engineer will discover that a very small quantity of clay impairs the strength of his concrete. He will therefore proceed to wash his gravel. He will not merely curse the clay. He will not try to educate it

out of the gravel. So our ecological engineer will recognize the ubiquity of *Homo's* rationalizations, and that these are protective devices used to dilute facts to non-toxic concentrations."

IDEA SUCCESSION

During his last two years Lovejoy focused his mind on a single problem: the succession in ideas about land-use. Just as there are predictable sequences in the development of plant and animal communities, knowledge of which is essential to agriculture and forestry, so, he argued, there may be predictable sequences in human thought about land-use, knowledge of which may be important to good administration, extension, and research.

Lovejoy postulated that ideas are conceived, born, grow up, have offspring, become senescent, and die, and that these developmental phases may have identifiable characteristics useful in forecasting the future or in interpreting the past. The successive phases may also have characteristic durations, possibly amenable to partial control. In a letter (3/19/41) he cites the following history of the deer problem in Michigan as a sample of the raw material from which a theory of idea-succession might be deduced:

1. From first talk of starvation in deer yards to first hay hauled	25–50 years
2. From this to first technical investigation of yards and the first post-mortems on dead deer	5 years
3. From this to competent surveys of all yards (via ineffective digressions such as hauling hay, or removing excess by trapping or by stunning with "mercy bullets")	3 years
4. From this to competent censuses of deer populations with tallies showing sex and age composition	3 years
5. From this to official recognition that there must be more legal kill or else wholesale starvation; that populations have outstripped their winter food and must go down	2 years
6. From this to start of systematic education to modify the buck law, which inhibits increasing the legal kill	2 years
7. From this to first sportsman-support in asking the legislature to "git modern in re deer"	2 years
Total elapsed time in idea succession, items 2 to 7, to date	17 years

Lovejoy then projects the possible future sequence:

8. From asking to getting legislative repeal of buck law and authority for "local regulation"	4– 6 years
9. From getting authority to learning how to use it	5–10 years (?)
10. Recognition of fire as a tool for increasing deer food on areas submarginal for forestry	10–25 years (?)
11. Evolution of techniques combining local deer regulation, forestry, and fire as a tool	? years

I think Lovejoy regarded this sequence of events as comprising a single stage in the intellectual succession. Through it runs one idea: too many deer. It grew up under the dominance of a preceding idea (too few deer), just as the forb stage grows up under the dominance of weeds, or the grass stage grows up under the dominance of forbs. It will be succeeded by another idea: regulated deer, locally adjusted to the needs and tolerances of forestry and other land-uses. Too few deer, too many deer, and an adjusted deer herd are three overlapping stages in a succession.

Within the present stage, Lovejoy considered hay-hauling, trapping, and mercy-bullets as digressions and evasions arising from public abhorrence of factual truth, i.e., as criteria of "youth" in the idea of too many deer. Items 4–7 represent education of the public, by slow degrees, to accept the factual truth already evident in item 2. Ecological engineering (i.e., "placing another banana-peel where it will do the most good") might, he thought, have hastened ultimate public acceptance.

Research on excess deer, Lovejoy points out, began in item 2 and reached print in item 6. But research, he says, has only begun when published:

"It's certainly urgent to get the infant-project born right, washed up, and crying good, but that's just a stage in raising a

family. Field work is gestation, publication is parturition, but getting into action is growing up. Research is grown when it has reached self-tending status, along with other kids of that generation."

LOVEJOYIANA

For those unfamiliar with Lovejoyeese, I present a few selected idioms and a few characteristic quotations:

pack-ratting: collecting reprints "in the standard campus manner"
terra-tinker: a land-use expert
barber shop biologist: a sportsman
mirabile dictuing: telling tall tales
rat-hole project: an ill-conceived official undertaking
sacred sawloggers: forestry propagandists
section 28: lower right abdomen
Novos, Demos, and Buros: researchers, politicians, and bureaucrats; novos nest in litters of old papers, from which, at irregular intervals, they hatch out monographic young.
"Sic 'em summa cum laude": citation granted to able critics
words with high muzzle-velocity: good writing
clubs: "There are three kinds of clubs. One kind peels all its birches, another only a few, another puts white paint on the scars of the old peelings." (letter 7/24/38)
research: "Hire a dozen techs. Turn 'em loose and they'll smell out, trail, and flush facts, fetch 'em home, and lay 'em on the hearth all-same cat and field-mouse. When they lay another separate on the Altar of Research, they have done their stuff. It's up to somebody else to carry on from there." (letter 9/22/40)
appetite: "As a kid I often ate all the apples I could, but never as many as I wanted to."
theses: "Theses for higher degrees in Ecological Engineering should weigh at least three pounds."
critics: "If they do it vicious-like, with teeth showing, they are surprised and amused to find that (the sacred cows) are easy scared, and run away with even a little roughing. So a few of us have quite a little fun yapping and nipping and shagging (them) around, letting on we're after hot blood right outa the neck." (letter 9/22/40)
carrying capacity: "The ultimate question is not how to step up human carrying capacities per habitat but what sort of humans we want to have around at all." (letter 9/22/40)

RECENT PUBLICATIONS BY P. S. LOVEJOY

1926. The worst-first theory. Journ. Forestry, 24: 351–7.
1933. Concepts and contours. Journ. Forestry, 31: 381–91.
1933. Fericulture. Univ. of Mich. Forest School Annual, pp. 12–13, 33.
1935. Ecological engineering. Mich. Acad. Sci. Arts and Letters, Ann Arbor, Ann. Repts., pp. 76–86.
1936. Harmonizing conflicting interests in land management. Proc. First N. Amer. Wildlife Conference, pp. 260–7.
1938. [Letter to Silcox.] Journ. Forestry, 36: 628–34.

In conclusion, I venture the personal opinion that the professions of forestry and wildlife management, as now constituted, will one day be adjudged to have been deficient in critics. If I am right in this, then P. S. Lovejoy, as one of our best critics, will grow in stature with the years.

In any case he did his valiant best to find new wedges, and season-checks to set them in, and to split new slabs of savvy off the big chunk.—ALDO LEOPOLD, *Madison, Wis.*